

EVOLUTION AND ADAPTIVE RADIATION
OF
BROMUS L. SECT. *GENEA* DUM. (POACEAE)

BY
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Then he gave a heap o' rules,
For the use o' learned fools,
"But nane o' them", said he, "is perfect to decide 'em".
Hech! I thocht o' Noah's ark
And the grand old patriach,
An' I wunnered how he managed to divide 'em.

.....

cont.

CONTENTS

1. ABSTRACT	1
2. INTRODUCTION	3
3. TAXONOMIC HISTORY	
3.1 Introduction	6
3.2 The circumscription of the genus <i>Bromus</i>	9
3.3 Infra-generic classification	10
3.4 History of section <i>Genea</i>	12
4. MATERIAL AND METHODS	
4.1 Sources of plant material	20
4.2 Experiment of phenotypic plasticity	21
4.3 Leaf anatomy	24
4.4 Surface characters as shown by scanning electronic microscopy (SEM)	25
4.5 Serology	28
4.6 Cytotaxonomy	31
5. TAXONOMY	
5.1 The <i>Bromus tectorum</i> - <i>B. sericeus</i> complex	41
5.1.1 Introduction	41
5.1.2 Taxonomy	43
5.1.3 Morphology	59
5.1.3.1 Historical	59
5.1.3.2 The present analysis	63
5.1.3.3 Notes on particular features	75
5.1.3.4 A phytogeographical note	84
5.1.4 Geography and ecology	85
5.1.5 Subsp. <i>tectorum</i> and subsp. <i>lucidus</i> and their relationship to <i>B. pectinatus</i> and its allies	93
5.1.6 Evolution and adaptive radiation	96

5.2	<i>Bromus sterilis</i> and the <i>B. diandrus</i> - <i>B. rigidus</i> complex	99
5.2.1	Introduction	99
5.2.2	Taxonomy	100
5.2.2.1	<i>B. sterilis</i>	100
5.2.2.2	<i>B. diandrus</i> - <i>B. rigidus</i> complex	109
5.2.3	Morphology	122
5.2.3.1	Historical	122
5.2.3.2	The present analysis	126
5.2.3.3	Notes on particular features	129
5.3	<i>Bromus madritensis</i> , <i>B. haussknechtii</i> , <i>B. rubens</i> and <i>B. fasciculatus</i>	135
5.3.1	Introduction	135
5.3.2	<i>B. madritensis</i> , <i>B. haussknechtii</i> and <i>B. rubens</i>	136
5.3.3	<i>B. fasciculatus</i>	139
5.3.3.1	Taxonomy	139
5.3.3.2	Morphology	144
5.3.3.2.1	Historical	144
5.3.3.2.2	The present analysis	148
5.3.3.2.3	Notes on particular features	149
5.4	Key to species of sect. <i>Genea</i>	153
6.	MICROMORPHOLOGICAL CHARACTERS	
6.1	Leaf anatomy	156
6.1.1	Introduction	156
6.1.2	Results	157
6.1.3	Discussion and Conclusions	162
6.2	Surface characters as shown by scanning electronic microscopy (SEM)	168
6.2.1	Introduction	168
6.2.2	Results	169
6.2.2.1	General descriptions of epidermis and notes on particular features	169
6.2.2.2	Form and function: an SEM investigation	175
6.2.3	Conclusions	179

7. CHEMICAL CHARACTERS

7.1	Introduction	188
7.2	Results	192
7.3	Discussion	192
7.4	Conclusions	200

8. CYTOLOGICAL CHARACTERS

8.1	Introduction	202
8.2	Objectives	211
8.3	Results	211
8.4	Discussion and conclusions	213
8.5	Further lines of research	219

9. EVOLUTION AND ADAPTIVE RADIATION

9.1	Introduction	223
9.2	Evolution of <i>Bromus</i> in Eurasia	228
9.3	Evolution and adaptive radiation in sect. <i>Genea</i>	232
9.4	Conclusions	254

10. REFERENCES

259

11. APPENDICES

274

12. PROOF COPY: Sales, F. (1991). A re-assessment of *Bromus tectorum*:
a computer analysis, synaptospermy and chorispermy.
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295

FINIS

302

CHAPTER 1. ABSTRACT

The 8(-9) annual species of *Bromus* generally placed in sect *Genea* were investigated taxonomically and biologically with the aim of improving their classification and giving a better understanding of their morphology and relationships. The species are widely distributed in the Mediterranean countries, SW Asia and also in northern Europe; some are important introduced weeds in other regions of the world, mainly with a Mediterranean-type climate. None has previously been investigated throughout their total areas. In this multi-disciplinary approach, material falling into the following existing taxa were studied: *B. diandrus*, *fasciculatus*, (*haussknechtii*), *madritensis*, *rigidus*, *rubens*, *sericeus*, *sterilis* and *tectorum*. The investigation was based on: herbarium resources, field-work, an experimental plasticity study, geography/ecology, a computer analysis, anatomy, SEM studies, serology and cytology. For reasons of convenience the species were considered in 3 groups. In each of these, varying degrees of emphasis were given to the results of the different investigations listed above. In the *B. tectorum-sericeus* group, a computer analysis based on information from a very large number of herbarium specimens supported the recognition of one species with 2 subspecies (*B. tectorum* subsp. *tectorum* and subsp. *lucidus* Sales). In this group the taxonomic and evolutionary significance of the features of dispersal biology was stressed. In the *B. sterilis-diandrus-rigidus* group, it is shown that the existing typification of *B. sterilis* is incorrect. *B. diandrus* and *rigidus*,

so often recognized as independent species are here regarded as varieties of one species. In the last group (*B. madritensis* (*haussknechtii*), *rubens*, *fasciculatus*), particular attention was given to *B. fasciculatus*. Its uniform morphology is stressed; no infraspecific taxa are recognized within it.

Leaf anatomy was studied and described; no major or significant differences were revealed in the species studied. Micromorphology was investigated for many vegetative and floral parts of the plant. This showed, *inter alia*, that certain characters, such as the shape of the callus/scar, have previously been given undue emphasis. SEM studies provided a new insight into some characters of biological importance, including stomata on the awns and the incomplete development of callus at floret base on chorispermous plants. A chapter on cytology confirms previous records of chromosome number and describes an improved technique.

Serological studies of double diffusion confirmed the close relation of *Genea* species and supported in general the recognition of the 3 groups based on morphology. *B. sterilis* and *B. madritensis* are probably at the core of sect. *Genea* from which 2 evolutionary lines towards *B. diandrus* var. *rigidus* and *B. fasciculatus* developed. *B. tectorum* may represent a link between sect. *Genea* and *B. pectinatus* complex (sect. *Bromus*). These aspects are discussed in the chapter on adaptive radiation.

CHAPTER 2. INTRODUCTION

This thesis offers an analysis of the diversity, classification and adaptive radiation in *Bromus* sect. *Genea*. The work has involved a wide range of different kinds of study. These different facets are synthesized in a taxonomic sense in Chapter 5 and in an evolutionary context in Chapter 9.

Of all the annual bromes, the c.8 species that have been included in sect. *Genea* can, to some extent, be regarded as the most highly evolved in the genus. Certainly *Genea* has some of the advanced characters recognised as such in the grass family, but these characters are combined with primitive ones that are present throughout the genus (Hubbard, 1948; Davidse, 1987). This combination of primitive and evolved characters suggests that this group must be very old (c. Pleistocene, Stebbins, 1981) and stable for a long time, but has recently undergone a speed-up in evolutionary terms. This interpretation would be in total agreement with the incomplete species differentiation in the whole *Genea* group. In fact, the number and variety of intermediate plants between *rigidus* and *diandrus*, *diandrus* and *sterilis*, *sterilis* and *madritensis*, *madritensis* and *rubens*, *rubens* and *fasciculatus*, *tectorum* and "*sericeus*" gives the novice agrostologist the impression that there is a continuous range of variation from one extreme of the section to the other, with *tectorum* and "*sericeus*" more clearly differentiated. This situation has been aggravated by the lack of a detailed world-wide study of these species (the most recent taxonomic treatments of this group were made in Floras; Smith, 1985), which has deprived

taxonomists of a clear picture of the whole range of variation in the group. As a consequence keys in local floras are often not helpful and identification can be a nightmare. Only in this century have botanists learned that phenotypic variability can sometimes be determined to a great extent by the environment. As a consequence, small morphological variations have been re-assessed taxonomically, but in many cases it is still unclear which variation is due purely to phenotypic plasticity and which is genetically determined, eventually meriting taxonomic recognition (Bor, 1968 ; Smith, 1985).

The answers to all these questions and the clarification of the taxonomy of this group of plants is the aim of this thesis. But this immediate objective is embraced by a wider one. The study of a group of plants is not complete with the mere understanding of what they are in this "slice of time" that is the present. Also, the relationships established during the evolutionary process, the factors that determined this process and how evolution actually took place, have to be dealt with to complete any taxonomic work. This group of grasses, perhaps still actively in the early stages of differentiation, offers an ideal situation for the study of the routes and patterns of adaptive radiation on grasses.

Apart from the delightful intellectual exercise that such a study represents, there should be also very practical outcomes. Hopefully this will be a contribution to the effort that has been made to control some of these species in the areas where they are noxious weeds.

Throughout this thesis the species are frequently abbreviated as follows: DI - *B. diandrus* var. *diandrus*; FA - *B. fasciculatus*; LU - *B. tectorum* subsp. *lucidus*; MA - *B. madritensis*; RI - *B. diandrus* var. *rigidus*; RU - *B. rubens*; ST - *B. sterilis*; TE - *B. tectorum* subsp. *tectorum*. All specimens cited in this thesis were examined by myself.

CHAPTER 3.

3.1 TAXONOMIC HISTORY

3.1.1 INTRODUCTION

The word βρώμα (Broma) was originally used in ancient Greece to designate "solid food and meat". Because of the basic importance of cereals as a food source in the Middle East, the words βρώμα or βρόμος were used to designate a group of oat-like grasses. Theophrastus (c.371 B.C.), as far as we know, was the first person to use the word in a botanical context. In *Historia Plantarum* he designated a grass "*Avena (aegilops) verò α bromos veluti silvestria quaedam α immitia sunt*" (English translation, *Historia Plantarum*, Amsterdam, p.953, 1644) and (on p.958) there is an illustration of a grass called *Bromus sterilis altera festuca*. Theophrastus used the words *avena*, *bromos* and *festuca* to describe some grasses close to oats. The great respect which was accorded to him resulted in scholars who followed Theophrastus using the same names as he did. This is the reason why, for several centuries up to the time of Linnaeus, the three names above were often indiscriminately used to designate a large group of oat-like grasses. Linnaeus in *Genera Plantarum*, 5th ed., 1754, separated them clearly by giving them the generic names of *Avena*, *Bromus* and *Festuca*. He described *Bromus* the following way:

83. BROMUS.* *Mont.* 32. *Ægilops Dill* gen. 3.

CAL. *Gluma* multiflora, bivalvis, patens, flosculos in spicam colligens; *valvulis* ovato-oblongis, acuminatis, muticis, inferiore minore.

COR. bivalvis: *Valvula inferior* major, magnitudine & figura calycis, concava, obtusa, *Aristam* infra apicem rectam emittens, supra *aristam* bifida. *V. superior* lanceolata, parva, mutica.

STAM. *Filamenta* tria, capillaria, corolla breviora. *Antherae* oblongæ.

PIST. *Germen* turbinatum. *Styli* duo, breves, reflexi, villosi. *Stigmata* simplicia.

PER. *Corolla* arctissime clausa, adnascitur, nec dehiscit.

SEM. unicum, oblongum, tectum, hinc convexum, inde fulcatum.

It is not only Linnaeus' description that is important in understanding his generic concept of *Bromus*, but also the references he cites in the protologue. The first reference is to Monti's *Catologi Stirpium Agri Bononiensis Prodromus* ... (1719). Monti seems to have been the first botanist who associated the name "*bromus*" with plants regarded nowadays as members of the genus *Bromus*. The citation of "32" (see Linnaeus' description above) is a mistake; the correct reference is to "35". On page 35 Monti wrote about *Bromus* and referred to his Figures 1 and 3. Figure 1 is probably a spikelet of *B. sterilis* and it is possible that Figure 3 is another *Bromus* species.

In addition to this reference, Linnaeus refers to Dillenius and in the pre-1753 editions of *Genera Plantarum* there was also a reference to Scheuchzer. It is possible, but not indisputable, that the illustrations given by these two botanists cited by Linnaeus represent species of *Bromus*.

As a consequence of the uncertainties referred to above, the listing of the *Bromus* species in *Species Plantarum* 76 (1753) is very important in understanding Linnaeus' concept of the genus. Linnaeus recognized 11 species in *Bromus*: *B. secalinus*, *B. squarrosus*, *B. purgans*, *B. ciliatus*, *B. sterilis*, *B. arvensis*, *B.*

tectorum, *B. hordeaceus*, *B. giganteus*, *B. pinnatus* and *B. aristatus*. The last 3 species are now included in other genera, respectively: *Festuca gigantea* (L.) Vill., *Hist.Pl.Dauph.* 110, 1787; *Brachypodium pinnatum* (L.) Beauv., *Agrost.* 101, 155, 1812; and *Agropyrum aristatum* (L.) Gaertner, *Novi Comment.Acad.Sci. Petrop.* 14: 540, 1770.

From Linnaeus' time till the present the genus *Bromus* has been dramatically enlarged, at least in terms of named taxa (Appendix 3.1). The pre-Darwinian concept of the immutability of taxa influenced taxonomists until comparatively recently. As a consequence, they attributed taxonomic rank to even minor phenotypic differences. Applying this old-fashioned concept, especially to annual species that present great phenotypic plasticity of vegetative parts and show numerous intermediate morphologies between species, resulted in a marked polytypism, especially at infraspecific levels. The polytypism of the last century found echoes in some modern taxonomists such as Maire & Weiller (1955). Nowadays, however, it is generally accepted that species are based, for the most part, largely on reasonably substantial genetic discontinuities and not on the amount of phenotypic differences between extreme typical variants (Turesson, 1931; Clausen *et al.*, 1940; Heslop-Harrison, 1953; Bradshaw, 1965). The general polytypism has been aggravated in *Bromus* by the lack of a global monographic study that would cover the whole range of distribution of some of the most critical species or, ideally, the genus in general. As a result of these deficiencies the total number of well-founded "good" species is still uncertain although some botanists give much higher numbers (e.g. Soderstrom

& Beaman, 1968, who refer to 200-400). I believe it is not much more than 100.

3.1.2 THE CIRCUMSCRIPTION OF THE GENUS *BROMUS*

Bromus includes annual and perennial species, typically of the temperate areas of Eurasia and America. Its highest diversity occurs in Eurasia, especially in SW Asia where it is believed to have originated (Stebbins, 1981). Occasionally it grows above the arctic circle; it is also in tropical areas at mountain-subalpine altitudes. It is wholly introduced and naturalized in other temperate areas, such as Australasia.

Two characteristics easily recognisable may be added to the Linnaean generic description: the starch grains are simple in *Bromus* (as in *Triticeae* and *Brachypodium*), but compound in *Festuceae* (Nägeli, 1858) and the top of the ovary is surmounted by a bilobed hairy appendage that remains attached to the caryopsis and from which the styles emerge laterally (Cugnac, 1945).

To the comprehensive description of the genus given by Smith (1970) I would add a few other particularities that characterize *Bromus* and separate it from close allies. A morphological feature which usefully separates the genus from *Festuca* is the sub-terminal position of awns in *Bromus*. Smith (1969^b) notes the serological isolation of *Bromus* from other, otherwise superficially similar, genera (e.g. *Brachypodium*). Harberd (1972) notes that *Bromus* has a mesocotyl development distinctively different from that of *Brachypodium*. The milky stage before the formation of the starch grains during the maturation of the caryopsis is much more extended in *Bromus* than in grasses in

general. This stage is easily recognisable because the grain is green, milky and shiny.

The genus seems isolated within its tribe - *Bromeae* - with only one other genus, *Littledalea* Hemsley (Smith, 1970) from C Asia to Western China. The latter differs from *Bromus* by its large ligulate, papery lemmas with erose tips and overlapping sheaths.

3.1.3 INFRA-GENERIC CLASSIFICATION

Influenced by the wide range of morphological variation, many taxonomists divided *Bromus* L. into smaller groups which were given the ranks of genus, subgenus or section. Table 3.1 lists some of the most significant taxonomic treatments; for a list of references see Smith (1970).

The most comprehensive classification of *Bromus* s.l. into smaller segregate genera was made by the Soviet taxonomists Nevski (1934) and Kreczetovich & Vvedensky (1934). To the present time, their opinions have only been followed by other Soviet taxonomists, e.g. Tsvelev (1984). Most non-Soviet botanists have not divided *Bromus*, with the surprising exception of Clapham, Tutin & Warburg, *Flora of the British Isles*, 1962; here they recognized the genera *Zerna*, *Anisantha* and *Bromus*. More generally, the subgroups in *Bromus* s.l. have been regarded as subgenera or sections and accepted as such. Some taxonomists such as Nikiforova (1968) and Meikle (1985) do not recognize any infra-generic taxa in their treatments of *Bromus*.

TABLE 3.1. Some of the most significant classifications where Bromus s.l. is divided into groups of different taxonomic rank. Capitals indicate groups regarded as genera by their authors.
 1) Smith in 1985a placed B. pumilio in a separate group (sect. Boissiera).
 For more complete references see Stapf (1928) and Smith (1970)

Genus		Subgenus		Section		
Panzer (1813)	Nevski (1934)	Hackel (1887)	Krecz. & Vved. (1934)	Dumortier (1823)	Tournay (1961)	Smith (1970)
ZERNA	ANISANTHA	Stenobromus	Stenobromus	Genea	Genea	Genea
	ZERNA	Festucoides	Zerna	Bromopsis Pnigma	Bromopsis	Pnigma
BROMUS	BROMUS	Zeobromus	Zeobromus	Bromium	Bromus	
MICHELARIA				Bromus		
BOISSIERA		BOISSIERA				
CERATOCHLOA	Ceratochloa	CERATOCHLOA		Ceratochloa		
NEVSKIELLA	Nevskiella		Nevskiella			
TRISETOBROMUS			TRISETOBROMUS		Neobromus	
LITTLEDALEA		LITTLEDALEA				

3.1.4 HISTORY OF SECTION *GENEA*

For a long time, the species that are investigated in this thesis have variously been given generic, subgeneric and sectional status for which the correct names are respectively *Anisantha*, *Stenobromus* and *Genea* (Table 3.2). Other names used are listed in Table 3.3.

Although *Zerna* Panzer was the first genus segregated from *Bromus* s.l. including some *Genea* species (*madritensis*, *sterilis* and *tectorum*) and the type species proposed for it was *B. sterilis* (Hitchcock, U.S. Dept. Agric. Bull. 772:24, 1920), the name *Zerna* has generally only been used for *Genea* species by some Soviet taxonomists. This name has been correctly rejected or neglected because, apart from the *Genea* element, it originally included many foreign elements from *Bromus* sect. *Pnigma* and the genus *Festuca*; and the only illustration in the original publication is, in any case, probably not a species which would be referred to sect. *Genea*.

Contrasting with the earlier lack of agreement concerning the taxonomic rank given to sect. *Genea* (or indeed other groups within *Bromus* s.l.), for the last 10-20 years almost all taxonomists have restricted themselves to using sectional status, e.g. Bor (1970), Smith (1981, 1985) and Clayton & Renvoize (1986). For a more comprehensive list of references see Table 3.4.

It was Dumortier (1823) who, for the first time, divided *Bromus* s.l. into sections: sect. *Genea*, sect. *Bromopsis*, sect. *Pnigma* and sect. *Bromium*. According to the *International Code of Botanical Nomenclature*, Art. 22.1 (1988), *Bromium* must nowadays be called *Bromus* because "The name of any subdivision of the genus

that includes the type of the ... genus is to repeat that generic name unaltered".

A criticism must be made of Dumortier's description of his sections: apart from sections *Bromus* and *Pnigma* he does not use the same characters throughout to define the sections. It is, therefore, very difficult, or impossible, to compare and contrast them. However, because of the way he presents and describes these sections it is my belief that each sectional description excludes the following ones. If my interpretation is correct, Dumortier could have keyed out the four sections as follows:

1. *Paleola exterior in setam canaliculatam desinens*,
apice bilaciniatasect. *Genea*
 + Species that do not present the above characters 2
2. *Seta fere terminalis, basi per apicem paleolae*
biaurita..... sect. *Bromopsis*
 + Species that do not present the above characters 3
3. *Axis basi circumscutatus, seta dorsalis* sect. *Pnigma*
Seta dorsalis, axis dorso continuus sect. *Bromium*

In the descriptions of the sections, Dumortier uses two expressions difficult to understand: "*axis basi circumscutatus*" and "*axis dorso continuus*". For a correct interpretation of them it is necessary to understand what Dumortier means by "*axis*" throughout his work on grasses. I agree with Tournay (1961) that these two expressions must be interpreted respectively as: "dorsal surface of glumes separated from the pedicel of the spikelet by an annular strangulation" and "dorsal surface glumes joining the pedicel

TABLE 3.2. Correct (i.e. earliest legitimately valid published (International Code of Botanical Nomenclature, Art. 11.3, 1988) names of sect. Genea at different taxonomic ranks, their place of publication and respective type species.

Rank	Name	Place of Publication	Lectotype		Origin of name
			Species	Authority	
Genus	<u>Anisantha</u> C. Koch	Linnaea, 21:394 (1848)	<u>A. tectorum</u> (L.) Nevski; syn: <u>A. pontica</u> C. Koch	C. Koch (1848)	From the greek "aniso" (= unequal) + anther meaning "a different number of anthers", 3 or <u>2</u> .
Subgenus	<u>Stenobromus</u> (Griseb.) Hackel	Engl. & Prantl, Nat. Pflanzenf. ed. 1, II, 2, p. 75 (1887); without reference to Grisebach	<u>B. rigidus</u> Roth	Rothmaler in Roem. & Usteri Mag. Bot. 4, 10: 21 (1790)	From the greek "stenos" meaning narrow, reference to the narrow glumes and lemmas
Section	<u>Genea</u> Dum.	Obs. Gram. Fl. Belg. p. 116 (1823)	<u>B. sterilis</u> L.	Tournay, Bull. Jard. Bot. Etat, 31: 294 (1961)	From the greek <u>γενεῖαν</u> meaning beard; "bearded inflorescences", reference to the long awns

TABLE 3.3. The names of subdivisions of *Bromus* s.l. that included § *Genea* species. Authors, place of publication and species included in each subdivision are indicated.

* indicates the presence of non § *Genea* elements in the original description

Author & Date	Place of Publication	Name (Rank)	Genea species included
Panzer (1814)	Denkschr.Muench. 1913: 297	<u>Zerna</u> (Genus)	madritensis sterilis tectorum *
Dumortier (1823)	Obs.Gram.Fl.Belg. :116	<u>Genea</u>	rigens, rigidus, sterilis, tectorum
Fries (1843)	Bot.Nat.1843: 131	<u>Annui</u> (Section)	sterilis, tectorum
Grisebach (1844)	Spic.Fl.Rum.Bith. II:448	<u>Stenobromus</u> (Section)	madritensis, maximus, sterilis, tectorum
Cosson & Germain (1845)	Fl.Env.Paris, ed.1: 643	<u>Annui</u> (Section)	sterilis, tectorum*
Fries (1845)	Sumnea Veg.Scand. I:76	<u>Vulpioides</u> (Section)	sterilis, tectorum
C. Koch (1848)	Linnaea 21: 394	<u>Anisantha</u> (Genus)	pontica (= tectorum)
Grisebach (1853)	Ledeb., Fl.Ross. 4: 359	<u>Schedonorus</u> (Section)	madritensis, maximus, rubens, sterilis, tectorum*
Cosson & Durieu (1855)	Fl.Alg.Phan.Glum. 157	<u>Eubromus</u> (Section)	fasciculatus, madri- tensis, rigidus, rubens, sterilis, tectorum
Nyman (1855)	Syll.Fl.Europ.: 419	<u>Schedonorus</u> (Subgenus)	madritensis, maximus, fasciculatus, rigidus, rubens, sterilis, tectorum*
Kirschleger (1857)	Fl.Als. 2: 348	<u>Trespa</u> (Section)	sterilis, tectorum
Jessen (1863)	Deutschl.Grass: 170	<u>Sterilis</u> (Section)	sterilis, tectorum
Hackel (1887)	Engl.et Prantl.,Nat. Pflanzenf.ed.1,II,2:75	<u>Stenobromus</u> (Subgenus)	sterilis, tectorum
Rouy (1912)	Soc.Sc.Nat.Char-Inf., Ann., 1912,Suppl.246	<u>Eubromus</u> (Subgenus)	madritensis, rubens tectorum, villosus*

without strangulation". However, this character does not seem very appropriate because I have observed a strangulation not only on specimens of sect. *Phigma*, but also those of other sections.

Apart from these negative aspects, Dumortier's descriptions of the sections are based on very few characters. Nonetheless, these are the earliest valid, legitimate sectional names.

Botanists, still convinced of the reality of the subgeneric divisions of *Bromus* and as their knowledge of the range of variation within it has increased, have been adding more characters to better define these subgeneric groups. The most complete description of sect. *Genea* was given recently by Smith (1985) in *Flora of Turkey*: "Annuals or biennials. Spikelets lanceolate when young, soon becoming cuneiform, broader at top, lower glume 1-veined, upper 3-veined. Lemma emarginate, rounded on back. Awn single, usually longer than lemma, flattened, rough, straight or rarely weakly out-curved, never twisted"; to which I add a few comments. These plants are basically annuals, only biennials with lateral growth when sometimes growing in wet places - not their native habitat. The awn is usually twisted once and it is not flat in section but canaliculate. This description does not include *B. sericeus* which has a higher number of veins on glumes (3 for the lower and 5 for the upper, as described in the literature, e.g. Bor, 1970; Cope, 1982; Tsvelev, 1984) because that species had not, at that time, been recorded from Turkey. In any case, my observations indicate that plants of other species of sect. *Genea* (e.g. *B. sterilis* and *B. rigidus*) can have 3/5 veins on the glumes and *B. sericeus* can have lower glume 5-veined and the upper 7-veined. In fact, the species of sect. *Genea* as a whole

can have as many veins on the glumes as any other section of *Bromus*.

I have accepted in this thesis the lowest taxonomic rank given so far to these species (section) because I do not think there is enough multidisciplinary data on the infragenic groups in *Bromus* to give them higher rank.

TABLE 3.4. Taxa recognised within sect. *Genea* in some of the most relevant taxonomic publications.

Author and Date of Publication	Place of Publication	Taxa of § <i>Genea</i> recognized	Generic/intra-genetic classification
Linnaeus (1753)	Sp.Pl.	<i>B. sterilis</i> <i>B. tectorum</i>	Genus <i>Bromus</i>
Boissier (1884)	Fl.Orient.	<i>B. fasciculatus</i> <i>B. flabellatus</i> <i>B. haussknechtii</i> <i>B. madritensis</i> <i>B. rigidus</i> <i>B. rubens</i> <i>B. sterilis</i> <i>B. tectorum</i>	Section <i>Eubromus</i>
Hayek (1933)	Pr.Fl.Pen. Balcanica	<i>B. fasciculatus</i> <i>B. madritensis</i> <i>B. rubens</i> <i>B. sterilis</i> <i>B. tectorum</i> <i>B. villosus</i>	Genus <i>Bromus</i>
Nevski (1934)	Sc.Herb.Fl. Asiae Med.	<i>A. gussonii</i> <i>A. madritensis</i> <i>A. rigens</i> <i>A. rubens</i> <i>A. sterilis</i> <i>A. sericea</i> <i>A. tectorum</i>	Genus <i>Anisantha</i>
Clap., Tut. & Warb. (1962)	Fl.Br.Isles	<i>A. diandrus</i> <i>A. madritensis</i> <i>A. rigida</i> <i>A. sterilis</i> <i>A. tectorum</i>	Genus <i>Anisantha</i>
Krecz. & Vved. (1934)	Fl. U.R.S.S.	<i>B. madritensis</i> <i>B. rigens</i> <i>B. rubens</i> <i>B. sericeus</i> <i>B. sterilis</i> <i>B. tectorum</i>	Subgenus <i>Stenobromus</i>
Ovad.-Yavin (1969)	Cyt. <i>Bromus</i> Palestina	<i>B. diandrus</i> <i>B. madritensis</i> <i>B. fasciculatus</i> <i>B. rigidus</i> <i>B. sterilis</i> <i>B. tectorum</i>	Subgenus <i>Stenobromus</i>

CONTINUED/

Author and Date of Publication	Place of Publication	Taxa of § Genea recognized	Generic/intra-genetic classification
Rechinger (1970)	Fl. Iranica	<i>B. diandrus</i> <i>B. fasciculatus</i> <i>B. madritensis</i> <i>B. rubens</i> <i>B. sericeus</i> <i>B. sterilis</i>	Section <i>Genea</i>
Smith (1981)	Fl. Europ.	<i>B. diandrus</i> <i>B. fasciculatus</i> <i>B. madritensis</i> <i>B. rigidus</i> <i>B. rubens</i> <i>B. sterilis</i> <i>B. tectorum</i>	Section <i>Genea</i>
Cope (1982)	Fl. Pakistan	<i>B. sericeus</i> <i>B. tectorum</i>	Section <i>Genea</i>
Tsvelev (1984)	Gr.Sov.Union	<i>A. diandra</i> <i>A. madritensis</i> <i>A. rubens</i> <i>A. sericea</i> <i>A. sterilis</i> <i>A. tectorum</i>	Genus <i>Anisantha</i>
Smith (1985)	Fl. Turk.	<i>B. diandrus</i> <i>B. fasciculatus</i> <i>B. madritensis</i> <i>B. rigidus</i> <i>B. rubens</i> <i>B. sterilis</i> <i>B. tectorum</i>	Section <i>Genea</i>
Feinb.-Dothan (1986)	Fl. Palestina	<i>B. diandrus</i> <i>B. fasciculatus</i> <i>B. madritensis</i> <i>B. rigidus</i> <i>B. rubens</i> <i>B. sterilis</i> <i>B. tectorum</i>	Section <i>Genea</i>

CHAPTER 4. MATERIAL AND METHODS

Except for a representative number of herbarium specimens cited under *B. tectorum* subsp. *tectorum* and subsp. *lucidus* (Chapter 5.1), *B. diandrus* var. *diandrus* and var. *rigidus* (Chapter 5.2) and *B. fasciculatus* (Chapter 5.3), all the material and methods for this thesis are described in this Chapter. A further exception is that of the computer analysis which is described in Chapter 5.1 and Appendix 5.1.1.

4.1 SOURCES OF PLANT MATERIAL

Observations were made mostly on herbarium material, but fresh material grown in a glass-house was also used to a great extent. Field observations were also carried out.

The very large herbarium collections studied (c. 2500 specimens) covered the whole range of the geographic distribution of sect. *Genea*. Specimens from the following herbaria were studied: B, BG, BM, BR, C, COI, E, ELVE, FI, G, GB, GL, HUJ, K, KASSEL, KUH, KUWAIT, LE, LINN, LISE, LISU, M, MAF, O, OXF, P, PAD, PR, RAW, S, SOM, TARI, TCD, W, WU (codes following *Index Herbariorum*).

Plants were grown in a glass-house both at the University of Edinburgh, Department of Botany and the Royal Botanic Garden of Edinburgh for:

- (a) increasing the grain collection supplied by nearly 40 Botanical Institutions throughout the geographical area of the *Genea* species;
- (b) a phenotypic plasticity experiment;

(c) cytotaxonomic studies.

Observations were made in the wild in Edinburgh (*B. sterilis*) and Portugal (several species) in late spring 1988 - 89 - 90.

4.2 EXPERIMENT OF PHENOTYPIC PLASTICITY

Being annuals and occupying mainly an area of Mediterranean climate with strong seasonal changes, *Genea* species need a fast answer to the environmental pressures during their short life cycle of 2 seasons. An experiment of phenotypic plasticity in which plants of some species were grown in different environmental conditions, was carried out to assess to what extent the great morphological variability of *Genea* species is environmentally induced. That plasticity should play an important role in the morphological complexity of these plants was already suggested by Bor (1968), Esnault-Blanchard (1981), Esnault (1984) and Smith (1985).

Two experiments were carried out during the course of this study. In both, pairs of species likely to be confused due to great morphological variability were tested in different water and soil nutrient regimes. The first experiment involved 2 accessions of each *B. madritensis* and *B. sterilis*, but it failed because the treatments were extreme and the plants never flourished and many died. An improved experiment was later carried out involving 1 accession each of *B. diandrus* vars. *diandrus* and *rigidus*, *B. madritensis* and *B. rubens*. The plants obtained were used for consultation where relevant and are referred to in Chapter 5.

Plant material studied (stored at E):

B. diandrus var. *diandrus*: P.M. Smith collection, from England,
Suffolk (accession no. 1527)

B. diandrus var. *rigidus*: Collected by myself in Portugal,
Nazaré (accession no. 1647)

B. madritensis: P.M. Smith collection from S Spain
(accession no. 1552)

B. rubens 197571: P.M. Smith collection, Plant Germplasm
Quarantine Center, Beltsville,
Maryland, U.S.A., material originally
from Italy (accession no. 1629).

The set-up of the experiment is here described. John Innes
Potting Compost No. 0, 1 and 2 and coarse sand were used in
different proportions:

soil 3:1, 3 parts of J.I.P.C. No. 2
1 part of coarse sand

soil 2:2, 2 parts of J.I.P.C. No. 1
2 parts of coarse sand

soil 1:3, 1 part of J.I.P.C. No. 0
3 parts of coarse sand

The amount of nutrients incorporated in the soil was
calculated for 2 months. Then Hoagland's solution was added to
maintain the differences in nutrient concentration amongst the
treatments (Table 4.2.1).

Three grains were sown per pot (324 pots). Only the first
plant to germinate was kept. Until the first leaves were
completely formed, the water regime was the same for all plants in

TABLE 4.2.1 Nutrient regime for the plants grown in the phenotypic plasticity experiment after 2 months of growth.

Hoagland's solution (ml)	Times a week	Kind of Soil (see text for explanation)
100	2	3:1
100	1	2:2
0	-	1:3

the experiment, always keeping the soil moist. Differentiation of the water regimes followed and this is described below:

unrestricted water - soil always humid;

semi-restricted water - water when the soil is dry, but before plants start to wilt;

restricted water - water when the plants are about to wilt.

Plants were collected and pressed at the end of the vegetative stage, before the emergence of the panicle; collected at the flowering stage, when the panicle stops expanding; and collected at the seed stage, before the disarticulation of the spikelets.

4.3 LEAF ANATOMY

Plant material studied (housed at E and with 'sample' labels to indicate it was used in this study):

B. diandrus var. *diandrus*: Greece, Cos, Davis 40555; Lesvos, Edmondson E2192; Turkey, Davis 42002.

B. diandrus var. *rigidus*: Morocco, Davis 54243; Davis 53768; Davis D49407. Algeria, Davis 51497.

B. fasciculatus: Egypt: Davis 6592B; Libya, Davis 49954. Transjordan, Davis 8599.

B. madritensis: Greece, Tokmakia Isles, Edmondson E.2529. Iraq, W. Haines 371. Libya, Davis 50167. Morocco, Davis D48657.

B. rubens: Algeria, Davis 53370; Greece, Davis 54022; Davis 40548; Libya, Davis 50561; Morocco, Davis 53660.

B. sterilis: Bulgaria, 14 V 1975, Stoeva s.n.; Iraq, W. Haines 1615; Turkey, Davis 42096.

B. tectorum subsp. *tectorum*: Afghanistan, Hedge & Wendelbo W. 3247; Algeria, Davis 52584; Iran, Archibald 1291.

B. tectorum subsp. *lucidus*: Afghanistan, Hedge & Wendelbo W. 2722; Hewer, 1066. Kuwait, Rawi et al. 10666. Saudi Arabia, Collenette 4231.

The anatomy of leaves was studied in 3-5 different herbarium specimens of each *Genea* species. The middle portion of the second leaf below the panicle was used. Johansen's (1940) method was followed in general, but some modifications greatly improved the quality of the slides (Table 4.3.1).

4.4 SURFACE CHARACTERS AS SHOWN BY SCANNING ELECTRONIC MICROSCOPY (SEM)

Plant material studied:

B. diandrus var. *diandrus*: P.M. Smith collection, from England Suffolk; grown in the glass-house (accession no. 1527).

B. diandrus var. *rigidus*: P.M. Smith collection, collected by myself, from Portugal, S. Pedro de Moel; grown in the glass-house (accession no. 1645).

B. fasciculatus: P.M. Smith collection, from Italy, Catania; grown in the glass-house (accession no. 1559).

B. madritensis: P.M. Smith collection, collected in Portugal, Jeria, Coimbra; grown in the glass-house (accession no. 1523).

B. rubens: Sampled from Fl. Libya, Davis 50561 (E).

TABLE 4.3.1 Procedure of preparation of leaf sections for anatomical studies according to Johansen (1940)
(1) My own improvements on the Johansen's method
(2) Modification based on Metcalfe (1960)

Time	Procedure	Formula			
	The samples were placed in:				
1-2h	20% DECON detergent (1) washed in distilled water				
24h	F.A.A. (formalin acetic alcohol)(2).....	60% alcohol	90ml		
		acetic acid alcohol	5ml		
		formalin	5ml		
1½h	hydrofluoric acid (40%)				
6h	running water (washing)				
overnight	25% alcohol in vacuum (dehydration).....	H ₂ O	Methylated Spirit	2-Methylpropan-ol	Abs. Alc.
2h	50% " " " "				
2h	75% " " " "	25%	100ml	40ml	10ml -
2h	85% " " " "	50%	100ml	80ml	20ml -
2h	95% " " " "	75%	60ml	100ml	40ml -
overnight	100% " " " "	85%	30ml	100ml	70ml -
2h	2-Methylpropan-2ol in vacuum and water bath (55°C)	85%	-	90ml	110ml -
2h	fresh " " " " "	100%	-	-	150ml some
overnight	fresh " " " " "				
2h	1:1 of 2-Methylpropan-2ol and parafin				
2h	Parawax in water bath (58°C)				
2h	fresh " " " " "				
overnight	fresh " " " " "				
	Two leaf samples of each species were embedded in each wax block.				
	One block of each species was cut and mounted for sectioning on the microtome.				
	Sectioning				
	The ribbon was placed on a large drop of water covering most of a slide previously covered with glycerin albumen.				
	The slides were placed on warm table to let the ribbon spread.				
	The water was removed and the slide was warmed again until the wax melted (1).				
	The slides were placed in:				
3/4h	Xylol				
3/4h	Fresh xylol				
10min	Absolute alcohol				
3/4h	Safranin.....	1gr of Safranin O was dissolved in 48ml of aniline water and 52ml of methylated spirit were added. Aniline water: 8.5ml of aniline (fresh) were added to 500ml of distilled water at 70°C.			
10min	Methylated spirit				
10min	Absolute alcohol				
	The slides were mounted in Euparal.				

B. sterilis: P.M. Smith collection, collected by myself in Edinburgh (accession no. 1635).

B. tectorum subsp. *tectorum*: P.M. Smith collection, from Israel, Upper Galilee (accession no. 1563)

B. tectorum subsp. *lucidus*: Sampled from Fl. Afghanistan, Hewer 1066 (E).

In addition to these, other herbarium specimens were used to study the callus/scar shape at the floret base and disarticulation of the spikelets. The species studied were *B. diandrus*, *B. fasciculatus*, *B. sterilis* and *B. tectorum*. The specimens are housed at B, COI, E, HUJ, K, LE, PR and O and have "sample" labels indicating they were used in this study.

The plant material was used directly from herbarium specimens; where recent material was used it was previously pressed and dried.

The parts of the plants studied were: leaf sheath, leaf auricle, ligule, middle portion of the second leaf blade, pedicel just below the spikelet, lemma, base of floret, callus/scar area, rachilla segments, awn, palea, lodicules and grain.

The study of this plant material by SEM was carried out both in the Department of Botany, University of Edinburgh and at the Royal Botanic Garden, Edinburgh, and the procedure followed was slightly different in each case. In the Department of Botany the parts of the plants listed above were mounted on aluminium stubs using a special kind of highly conductive kind of glue (M-Glue for SEM Sample Mounting, G3664, AGAR Scientific Ltd); the specimens were earthed to the stub using Quick Dry Colloidal Silver (POLARON Equipment Ltd). The stubs were coated with gold using an Emscope

Sputter coater (Emscope Laboratories, Ashford, Kent, U.K.) for 3-5 minutes at 20mA, 0.08Torr, flushed with argon. The stubs were viewed using the Cambridge Stereo Scan 90B, Cambridge Instruments - LEICA Cambridge, at an accelerating voltage of 2-5KV. Electron micrographs were recorded on Ilford FP4 and Kodak Plus-X Pan 120 film. In the Royal Botanic Garden, the plant material was mounted on aluminium stubs using ordinary double-sided adhesive tape and no silver paint was employed. The stubs were coated with Palladium using an Emscope SB250 (Emscope Laboratories, Ashford, Kent, U.K.) for 3 min at 25mA, 0.1 Torr, flushed with argon. The stubs were viewed using the JEOL T200 Scan Electronic Microscope (JEOL, U.K. Ltd) at an accelerating voltage of 15KV. Electron micrographs were recorded on Ilford Panchrom film.

4.5 SEROLOGY

Plant material studied:

- B. diandrus* var. *diandrus*: P.M. Smith collection, from England, Suffolk (accession no. 1529) -DI₁a-g; collected by myself, from Portugal, S. Romão, S. Estrela (accession no. 1650) - DI₁a-g.
- B. diandrus* var. *rigidus*: P.M. Smith collection; collected by myself, from Portugal, Nazaré (accession no. 1647) - RI a-g & a-s.
- B. fasciculatus*: P.M. Smith collection, from Italy, Catania; grown in the glass-house (accession no. 1559) - FA a-g.
- B. madritensis*: P.M. Smith collection from Germany, Mainz; grown in the glass-house (accession no. 1570) - MA₁a-g; from Germany, Stuttgart; grown in the glass-house (accession no.

1579) - MA₂a-g & a-s.

B. madritensis subsp. *kunkelii*: P.M. Smith collection, sampled from Fl. Tenerife, Dickson 121 - MA_ka-g.

B. rubens 487414: P.M. Smith collection, Plant Germplasm Quarantine Center, Beltsville, Maryland, U.S.A., material originally from California (accession no. 1632) - RU a-g.

B. sterilis: P.M. Smith collection, from Edinburgh (accession no. 1636) - ST a-g & a-s.

B. tectorum subsp. *tectorum*: P.M. Smith collection, from Germany, Stuttgart, grown in the glass-house (accession no. 1581) - TE₁a-g & a-s; collected by myself, from Portugal, S. Estrela, Seia (accession no. 1652) - TE₂a-g.

B. tectorum subsp. *lucidus*: Sampled from Fl. Kuwait, Rawi et al. AR 1791, LU₁a-g and AR 1322, LU₂a-g (KUH).

Methods employed for antigen and antiserum preparation resembled those described by Smith (1972).

Antiserum preparation:

1. Mature florets were air-dried, immersed in 50% sulphuric acid for 20 min, the grains washed free of husk and acid and re-dried.
2. The grains were ground in an electric mill (Casella barley mill).
3. The globuline proteins were extracted from the grist in 1% sodium chloride solution at 4°C for 48 hours.
4. After centrifugation in the cold room in a Bench Centrifuge Callenkamp, 5000rpm, the supernatant was tested for protein concentration by the Lowry Standard Curve method and

adjusted to 1%. Dilution was by simple addition of 1% sodium chloride solution. Weaker solutions were placed in a Visking dialysis tube, tied off at each end, and immersed in a solution containing Carbowax 4000; in this way water was removed from the protein solution by osmosis.

5. These adjusted extracts were used to raise antisera in sheep, on a contract basis by The Binding Site Ltd., Birmingham. Antiserum was stored in frozen aliquots of 5ml at -40°C , until use. The solutions were preserved by the addition of 0.1% sodium azide as an antibacterial agent.

For antigen preparation the procedure above was followed, except that extracts of 0.5% protein concentration were produced. This economy of material was found sufficient to produce the strongest antiserum reactions encountered. Antigen solutions were kept in a refrigerator at $1-2^{\circ}\text{C}$ and shaken by hand before use - some protein aggregation and precipitation gradually occurred.

Antigens and antisera were allowed to react in agar gels (oxid immunoelectrophoresis agar 1.2% w/v, buffered at pH 8.2 by sodium barbitone HCl buffer, 1.7mm thick, on glass plates 10.2 x 8.2mm in size). Holes (0.02ml) and troughs (0.4ml) were cut in the agar to contain the reactants. Holes were filled with antigen solution and troughs with antiserum. Antigen-antibody reactions were visible after 8 hours and reached a maximum strength after 96 hours. At that time they were washed in gently running water for 48 hours to remove buffer salts and unreacted proteins. The plates were then covered with filter paper and allowed to dry out. The paper was then carefully removed and the gel fixed and stained for

5 minutes in 1% Ponceau S in 10% ethanoic acid. Differentiation, in running tapwater, took about 5 minutes. Finally, the stained preparation was dried once more, ready for analysis and photography. Photographs were taken on Kodak Technical Pan high contrast film and printed on Kodaprint No. 3 printing paper.

4.6 CYTOTAXONOMY

4.6.1 MATERIAL

Bearing in mind that at least to start with not all species would be studied I choose a representative group of species to work with according to the following criteria:

1. Species with high, medium and low chromosome number reported from literature.
2. Species from different morphological groups within the sect. *Genea*.
- especially those that are more likely to be misidentified.
3. Amount of caryopsides available.
4. Material of different provenance covering a wide geographical range, including some native and one certainly introduced (Table 4.6.1).

According to these parameters I tested different treatments on *B. diandrus* var. *rigidus* and *B. rubens*, with the work extended later to cover *B. madritensis*, *B. fasciculatus*, *B. sterilis* and *B. tectorum* (Table 4.6.1). Only one accession of each species was studied and only somatic chromosomes observed.

The parts of plants studied are indicated on Table 4.6.1 and reagents used for chromosome preparations on Table 4.6.2.

TABLE 4.6.1 Material examined for cytology by the present author,
its origin and part of the plant studied.

Species	Country	Accession No.	Part of plant studied
<i>B. diandrus</i> var. <i>diandrus</i>	England, Suffolk	1527	Root tip
<i>B. diandrus</i> var. <i>rigidus</i>	Portugal, Nazaré	1647	Root tip & leaf meristem
<i>B. fasciculatus</i>	Italy, Catania	1559	Root tip
<i>B. madritensis</i>	S Spain	1552	Root tip
<i>B. rubens</i> 487414	Plant Germplasm Quarantine Center U.S.A., originally from California	1632	Root tip
<i>B. sterilis</i>	Scotland, Edinburgh	1648	Young ovaries & anthers
<i>B. tectorum</i>	Portugal	1653	Root tip

Table 4.6.2 Reagents used in chromosome studies. The chemicals and their method of preparation are described in Appendix 4.1, the numbers in brackets are those of this Appendix.

Pre-treatment	Fixation	Storage	Maceration (Hydrolysis)	Staining	Softening of tissue	Temporary mounting	Permanent mounting
1-Bromona-phtalene (1)	Carnoy's (4)	Carnoy's	5N HCl	Lacto-propionic orcein (6)	Cellulase 4% (10)	Rubber solution (12)	Absolute alcohol
P-Dichloro-benzene (2)	Farmer's (5)			Acid acetic-orcein (7)	Pectinase 4% (11)	45% Acetic acid	Xylene
8-Hydroxy-quinoline (3)				Feulgen's (8)			45% Acetic acid
				SO ₂ water (9)			Paraffin
							Euparal

Photomicrographs were taken with an Olympus OM-2 camera attached to a Dialux 20 microscope using Kodak Technical Pan film developed with Kodak HC 110 dilution, 6 min.

4.6.2 METHODS

4.6.2.1 Cytological treatments

Several procedures were followed and the one described in Tab.4.6.3 was the one that proved to give the best results overall. The others are described in Table 4.6.4. Much material can be processed at the same time although more than two species are difficult to handle simultaneously.

Temporary slides were sealed with rubber solution and stored in a refrigerator at $+4.5^{\circ}\text{C}$ in aqueous vapour chamber. The procedure for making permanent slides was that of Bradley (1948).

4.6.2.2 Preparation of live material

Root tip chromosomes were counted in many cells of many plants of the same population. Less material of leaf meristem, ovaries and anthers was studied.

Root Meristems

Taxa studied: *B. fasciculatus*, *B. madritensis*, *B. diandrus* var. *rigidus*, *B. rubens* and *B. tectorum*.

(a) Germination

25-35 caryopsides were germinated in petri dishes with filter paper on the bottom and top lid, kept wet with tap water under the following conditions,

Table 4.6.3 Technique for preparing cytological slides for chromosome counting in root tips. To avoid confusion on labelling, material of the same species must be processed through all stages in the same vial carefully topped up (especially in steps nos. 1 and 6) to avoid evaporation of some volatile chemicals.

Technique stage	Steps	Time temperature	Observations
Fixation	1. Carnoy's fluid	at least 15 min. room temp.	Fixation is processed to - coagulate the cell constituents without disturbance of its structure; - improve reaction cell structure stain (mordanting); - alcoholic fixatives with acetic acids (such as this one) soften cell walls giving better squashes.
(Storage)	1.a. Carnoy's fluid	at least 15 min. room temp.	
Hydrolysis/ Maceration	2. 5N HCl	30 min. room temp.	HCl is essential for Feulgen's technique. It 1) frees by hydrolysis aldehyde groups of the DNA that then can react with the leuco-basic fuchsin of the Feulgen's reagent resulting in strong magenta-pink colour; 2) macerates plant tissues by loosening the middle lamellae, making squash easier.
	3. Wash in distilled water	1 min.	
Staining	4. Feulgen's reagent	30 min.	It gives a translucent but good stain and the cells are usually quite clear.
	5. Wash in distilled water	few min.	

6. SO ₂ water	3 x 5 min.	Bleaches the over-stained chromosomes making morphology clearer.
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7. Cellulase 4% Pectinase 4% (1:1)	Necessary for a good squash. Pectinase attacks middle lamella and so promotes cell separation. Cellulase attacks cellulose and so promotes cell flatness.
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8. Transfer the root to a slide	Now root length can be measured.
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9. Cut the densely stained root tip (top millimetre of the root and place it in a drop of 45% acetic acid	
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10. Cut the root tip in two and place both pieces a few millimetres apart	Less material gives a better squash.
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Squashing

11. Cover with a no. 0 cover-glass	When the maceration and softening are adequate the cover-glass weight is enough to squash the cells.
------------------------------------	--

12. Turn the slide up side down and press it against 3 sheets of filter paper	This improves squashing. Avoid lateral movement of cover-glass as this destroys cells.
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13. Turn the slide up again and tap the coverglass with blunt metal rod.	This must complete squash.
--	----------------------------

14. Heat the slide gently.	Causes the cells to swell and promotes good spreads.
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Table 4.6.4 Treatments used for cytological studies in root tips as alternatives to the one described in Table 4.6.3.

Technique stage	Steps	Time	Observations
Fixation	Farmer's reagent	at least 15 min.	
Pretreatment	i) 1-Bromonaphthalene	2h 6h 12h 24h room temp.	By inhibiting the activity of the spindle during division it accumulates divisions with the chromosomes scattered through the cytoplasm instead of aggregated on the equator. The chromosomes shorten and straighten more than normal due to over-contraction.
	ii) 8-Hydroxyquinoline	6h 24h room temp.	
	iii) P-Dichlorobenzene	4h 6h room temp.	
	iv) Cold treatment. Petri dishes with seedlings germinating were put in the fridge.	36h +4.6°C	
	Wash in water	few min.	
Staining	i) Lacto-propionic orcein according to Dyer (1963)		None of these stains require previous hydrolysis.
	ii) Acid-acetic acid orcein 1%. Place roots in the stain in a glass watch. Warm gently up to vapour. Squash in a drop of stain.		

- 1) normal day light and darkness (July/August, Edinburgh),
room temperature ($\pm 24^{\circ}\text{C}$);
- 2) dark, room temperature ($\pm 24^{\circ}\text{C}$), until germination starts
then followed by condition 1) above;
- 3) dark, 13°C until germination starts, then followed by
condition 1) above.

(b) Sampling of the material

To make possible later measurements, roots were cut close to the caryopsides. Different roots were sampled as follows,

- α) first root up to 2mm long;
- β) second root up to 2mm long;
- γ) first root excised when second emerges. Second root up to
2mm long was sampled;

and at different times of the day:

- I) morning (12.00);
- II) afternoon (18.00);
- III) night (12.00).

According to the different conditions of germination (see 1), 2) and 3) above) roots were sampled at different times (36-48h for conditions 1) and 2); 60-72h for condition 3)). Part of this material was fixed directly (control, Table 4.6.3). The other part was pretreated before fixation (Table 4.6.4). Different stains were used (Tables 4.6.3 and 4.6.4).

The number of cells observed in division is very variable, but in general quite low. To find the best conditions of germination and times of sampling the material in order to get the most active meristems, the following different combinations of the above conditions were tested:

1/ α /I

2/ α /I; 2/ α /II; 2/ α /III

2/ β /I

3/ α /I

3/ γ /I

Leaf Meristems

Taxa studied: *B. diandrus* var. *diandrus* and var. *rigidus*.

(a) Germination

Ten caryopsides were germinated in petri dishes with filter paper on the bottom and top lid, kept wet with tap water in normal day light and darkness (July/August, Edinburgh) at room temperature ($\pm 27^{\circ}\text{C}$). After 7 days of germination the first leaf is already long enough to manipulate ($\pm 6\text{cm}$ long) but not completely mature, so the meristem is still active.

(b) Sampling of the material

The procedure for dissection of the seedlings for its leaf meristems was modified from Bennett, 1964. The base of leaf was fixed directly and then stained in Feulgen (Table 4.6.3).

Ovaries and Anthers

Species studied: *B. sterilis*.

Plants were collected in the field, put in a jar with water and half an hour later young florets were dissected at the dissecting microscope. Ovaries and anthers were sampled, fixed in Farmer's fluid and stored in a refrigerator at $+4.5^{\circ}\text{C}$ for several weeks. They were stained in Feulgen (Table 4.6.3), some treated with enzyme, others not.

4.6.2.3 Vouchers

Five plants per species, one plant per pot were sown in John Innes Potting Compost No. 1 in the glasshouses of the Royal Botanic Garden Edinburgh on 26/7/89. When mature they were pressed, mounted and deposited in the Royal Botanic Garden Edinburgh Herbarium (E).

4.6.2.4 Photography and drawing techniques.

Photographs were taken before making the slides permanent. Yellow-green filter was used. Photographs were printed in duplicate; one for illustration, the other as basis for an interpretative drawing according to Manton (1950). The chromosomes were inked on the latter which was then bleached - the image disappears but the diagram remains. These drawings were made, observing the slide at the same time. In some cases chromosomes present in the cell were not clearly photographed because they were in a different plane. In these cases they were included in the drawings. Most of the figures drawn and photographed were metaphase plates, suitably squashed and dispersed.

CHAPTER 5. TAXONOMY

5.1 THE *BROMUS TECTORUM* - *B. SERICEUS* COMPLEX

5.1.1 INTRODUCTION

The plants of the complex *B. tectorum* L./*B. sericeus* Drobov occupy a distinct position in *Bromus* sect. *Genea* because of their elegant, slender, 1-sided panicles, the silvery appearance of the spikelets, the great variation of vein number on the glumes (1, 3, 5 on the lower ones; 3, 4, 5, 7 on the upper ones) and a clear tendency to synaptospermy.

In Eurasia, the area of maximum morphological diversity and probably the centre of origin of the complex, it extends from Macaronesia, throughout Europe, N Africa, SW Asia to the Himalayas, not penetrating deeply into the Arabian Peninsula and becoming very rare in C Asia. It was introduced in N America as early as the 18th century, covering nowadays great stretches of land especially in the NW being there a noxious, invasive weed. It was introduced as well into Australia and New Zealand probably in the last century; here it is quite rare (Fig. 5.1.1).

B. tectorum was described from Europe and *B. sericeus* from Tashkent in Soviet C Asia. These taxa represent two well-defined extremes of a range of variation. Before the publication of *B. sericeus* in 1925 and even later, but before the great work that has been done in recent decades on the floras of SW Asia, *B. tectorum* was easily recognised and keyed out from the other *Genea* species. However, the study of *B. tectorum* and *B. sericeus* in places where both are likely to occur has shown a great number and diversity of intermediates for which the existing keys and Floras are, at best, not helpful. I eventually concluded that they could

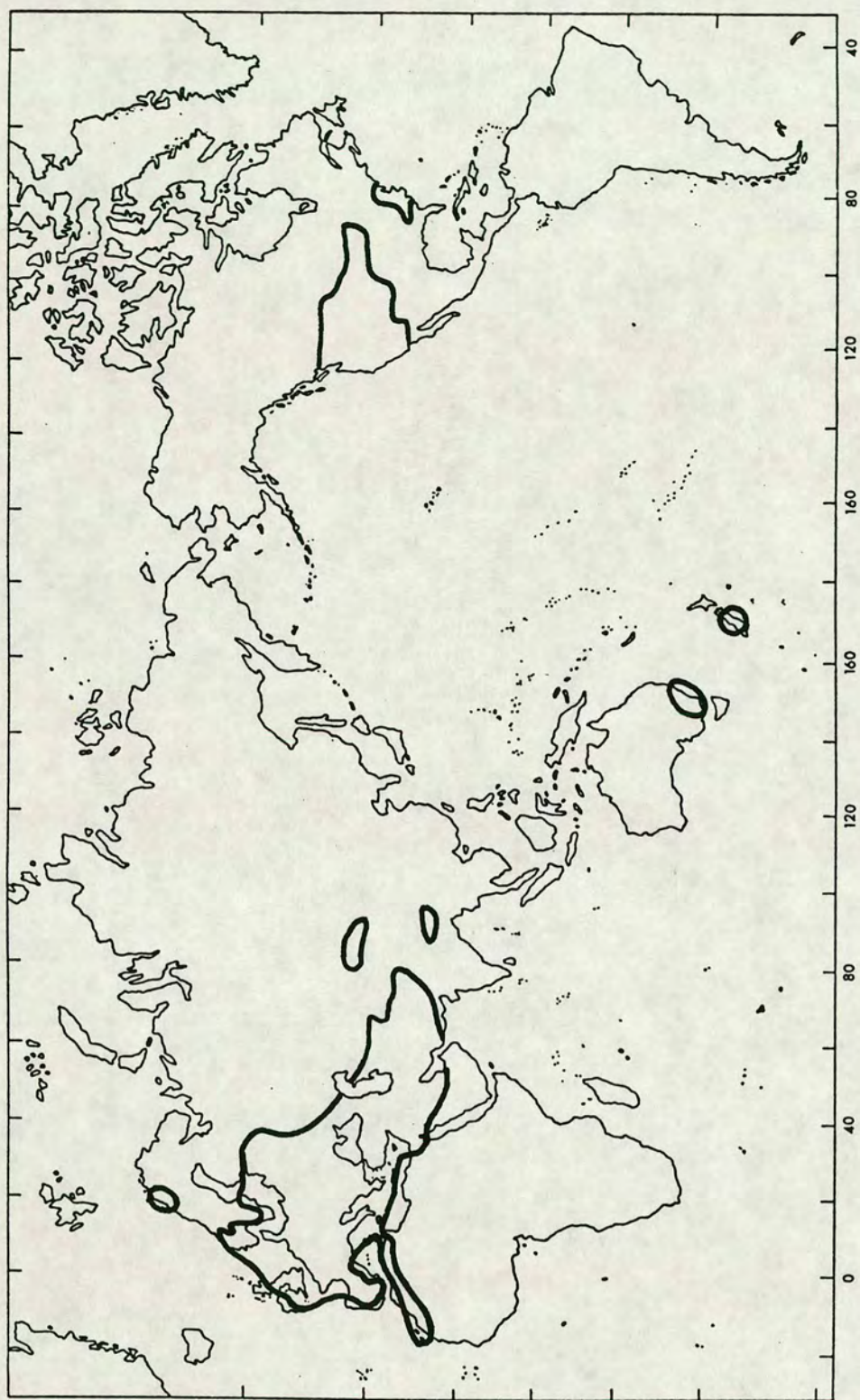


FIG. 5.1.1. Global distribution of *B. tectorum* L. including its 2 subspecies. In Australia, New Zealand, the New World and in parts of N. Europe the species is not native. All the plant material mapped was studied.

not be maintained as separate species, only as subspecies.

5.1.2 TAXONOMY

*B. tectorum** L., Sp.Pl.77 (1753).

Annual, 6-90cm tall, with solitary or loosely tufted, ascending to erect, slender culms, often minutely pubescent below the nodes and always so just below the panicle. Leaf sheath softly villous to pilose with retrorse patent hairs, apically glabrous or minutely pubescent; occasionally glabrous throughout; ligule fringed, acute or rounded at base. Leaf blade acuminate, 1.5-15 x 0.2-0.4 (-9.5)cm with short or long hairs, denser on the adaxial surface, very often with longer hairs along the margin continuing along the margin of the sheath near the ligule. Panicle condensed and ascending when young, soon becoming lax, nodding and clearly unilateral, deltoid or oblong in outline, 1-15cm long from the lowest to the uppermost node. Panicle branches slender, tortuous. Panicle axis and branches slightly to densely pubescent with short or long hairs. Branches longer to shorter than spikelets, with up to 5 ramifications, 0.6-8cm long. Spikelets 1-14 per branch, cuneate, broadening and shortening at maturity when the rachilla segments curve. Florets 5-17 per spikelet of which only 1-3 are fertile. Glumes and lemma pale green, often tinged with purple, with a broad hyaline margin giving a silvery/shiny appearance to the spikelets, usually with small scattered or dense longer hairs, more rarely glabrous. Lower glume narrowly lanceolate, 1-3-veined,

* "tectorum: of the roofs of houses"; which is clearly a secondary habitat for the species - even in Linnaeus' time.

5.7 x 1mm to 10.6 x 1.8mm; upper glume lanceolate, 3-7-veined, 8 x 1.6mm to 13.5 x 2.2mm. Lemmas of fertile florets 7-veined, 6.5-24mm long, 2-toothed at apex; lemma size and vein number decreasing considerably towards the top sterile, narrow-lanceolate, 1-veined florets. Awn straight, very rarely slightly curved, slender, often with a single twist, inserted 2.5-6mm below the lemma apex; awn length varying on individual spikelets: their apices either all notably at the same level or else somewhat irregular with the lowermost always much below the others. Awn of second floret 10-26mm long. Palea 6.8-14mm, shorter than lemma, glabrous on adaxial surface; abaxial surface glabrous or hairy with shorter or longer hairs, these sometimes present only between the veins and the margins; long, spreading hairs along the two veins, longer near apex. Stamens 3; anthers 0.5-1.3mm long. Caryopsides usually straight, sometimes slightly curved outwards, usually c. 0.2mm shorter than palea, sometimes as long, or c. 0.3mm longer. Callus of rachilla segments differentiated only below the upper sterile florets.

This is the most widespread species in sect. *Genea*, easily recognised by its slender, 1-sided nodding panicles and distinct and usually numerous sterile florets. The description above combines the two morphological extremes that have previously been given independent specific status: *B. tectorum* L., described from Europe, and *B. "sericeus"* Drobov from C Asia. The many intermediates between them are also covered in the description.

B. tectorum sensu stricto designates taller plants, with longer leaves, longer panicles, longer, thinner and more divided panicle branches, and with more spikelets; the spikelets being shorter, less shiny, with fewer florets. Glumes, lemmas, awns, paleas, grains and anthers are all smaller; the lower glume is 1-veined and the upper 3-5-veined. The sterile florets are more clearly separated from the fertile ones by a long rachilla segment. The awn is inserted closer to the lemma apex.

B. "sericeus" designates plants that are shorter with regard to the vegetative parts, but more robust-looking in reproductive ones, showing bigger structures. Its name comes from the more shiny appearance, a consequence of the proportionally larger hyaline margins and paler green colour on the spikelets. The lower glume is 3-veined and the upper 5(-7) veined. The awn extremities are more regular, almost as if cut with scissors at the same level.

The higher incidence and greater variability of intermediates between these taxa occur in the eastern mediterranean area, from Sinai and the N Arabian Peninsula to E Turkey. Westwards the plants tend to be more like typical *B. tectorum* described above. Eastwards, along the south of USSR, Iran, Afghanistan and NW of Pakistan it is possible to find the typical *B. "sericeus"*, and plants easily identified as *B. tectorum*; as well as some intermediates.

I have examined a very large number of specimens of this complex (many more than any previous workers, I believe) and the result of this detailed analysis clearly shows that it is impossible to maintain 2 independent species. Nevertheless, I was

convinced that there was a boundary between the two taxa. In the eastern part of the distributional area, mainly in more arid/xeric habitats and lower lands, completely synaptospermous plants can be found. In these the disarticulation of the spikelet occurs only below the lower floret so that the whole spikelet is dispersed as a unit. Because of the biological evolutionary importance of the development of new strategies for dispersal biology, combined with a geographical-ecological difference between the two taxa, I consider that the most practical taxonomic resolution of this interesting problem is to recognize two subspecies.

Key to the subspecies:

1.a. Lower glume 1-veined; rachilla callus well-differentiated below each fertile floret (chorispermous plants* - Figs 6.2.33-35)

.....*B. tectorum* subsp. *tectorum*

b. Lower glume 3-veined; rachilla callus well-differentiated only below the lowermost plant (synaptospermous plants -

Figs 6.2.38-40)

.....*B. tectorum* subsp. *lucidus* Sales

B. tectorum L. subsp. *tectorum*

Syn: *Zerna tectorum* Panz. in Denkschr.Akad.Muench. 1813: 297

(1814) - formal combination not made but clearly based on

Bromus tectorum L.;

B. scabriflorus Opiz in Naturalientausch. no.9; 119 (1825).

* See 5.1.3.3 for an explanation of the term.

Type: "Bohemia, loc. illegible, Opiz
[Herb.Cech.Mus.Nat.Prague, no. 495725c]."

Schedonorus tectorum (L.) Fries in Bot.Not. 9: 131 (1843);

Anisantha pontica C. Koch in Linnaea 21: 394 (1848). Type:
Turkey, Çoruh, Ispir - B (?†);

A. tectorum (L.) Nevski in Acta Univ.Asia Med. ser. 8b (Bot.)
17: 20,22 (1934).

Icon.: Sibthorp & Smith, Fl.Graeca 1: tab. 82 (1806); Ovchinnikov,
Fl. Tadjikistan 1: 257, tab. 33, fig. 1-3 (1957) - as
Anisantha tectorum; Hubbard, Grasses, 3rd edit., 62 (1985).
Penguin Books.

Type: Europe. LINN 93/25! - (Smith, 1985, p.500, designated this
specimen as lectotype).

Diagnostic features of the type specimen based on my own
observations:

Leaf blade length: 9-11.5cm

Panicle length: 8.5-9.2cm

Longest panicle branch in the lowermost panicle node: 4.9cm

No. of nodes in the panicle branch above: 1 node with 2
branches

No. of spikelets in the panicle branch above: 3

Panicle branches pubescence: short erect hairs

Spikelet length: 3.5 cm

No. of florets per spikelet: 6

Glume shape: lanceolate

Vein no. on lower glume: 1

Vein no. on upper glume: 3

2nd lemma length: 13mm

Top of spikelet including awns: irregular

Anther length: 0.7mm

Callus on rachilla at the base of each fertile plant: fully developed.

Habitats: from sea level up to 4000m; on chalk, gypsum, limestone, clay/igneous, volcanic ash, basalt, sandy or rocky soil; in semi-desert wadis, steppe, open woods or among shrubs in isolated areas or plantations, in very arid conditions but also irrigated fields, hill slopes, grasslands, meadows, roadsides, disturbed areas; in SW Asia often associated with *Juniperus polycarpus*, *Quercus aegilops*, *Q. coccifera*, *Amygdalus* sp., *Astragalus* sp., *Pistacia* sp. and *Populus*.

Selection of specimens studied. In the citation of specimens that follow, some are preceded by symbols (e.g. N, AS, HI, MA, etc.). These refer to the symbols used in the standard Floras of some countries or regions to designate particular geographic or phytogeographical areas. Herbarium symbols given in brackets are those used in *Index Herbariorum* ed.7 (1981). All specimens cited were seen.

EUROPE

Austria. Wien, near Nussdorf, 170M, *Keller* 5372 (E). Burgenland; near Neusiedl am See, *Jacobs* 5986 (BG).

Belgium. Goé, 18 v 1908, *Mairlot* s.n. (O).

Bulgaria. Turnovo, 14 v 1915, *Mruvicka* s.n. (SOM). Varna, 1896, *Javasott* s.n. (SOM). Sofia near Airport, 22 v 1977; *Vibodeevsky* s.n. (SOM).

Corsica. Propriano. Webster 14451 (E).

Czechoslovakia. Praha, 300M, *Rohlena & Domin* 712 (E). Brno, Cerná, c. 250M, 23 v 1947, *Jedlička* 1396 (E).

Denmark. Silkeborg, 9 vii 1883, *Holm* s.n. (O). Skanderborg, 7 vii 1971, *Løjtnant & Pedersen* 696 (O).

France. Auvergne: Puy de Dome, viii 1840, *J. Ball* s.n. (E). Paris, *Jervett* s.n. (E). Nantes, 28 vi 1954, *Stormer* (O).

Germany. Würzburg, c. 180M, *Botanische Vereinigung Würzburg*. 391 (BG). Karlsruhe, c. 117M, *Kneucker* 289 (O). Berlin, Potsdam, *J. Ball* s.n. (E). Hamburg, vii 1840, *Maly* s.n. (E-GL).

Greece. Psara Island, 10-100M, 22 iv 1973, *Greuter* 10978 (E). Porto hago, 22 iv 1965, *Coode & Jones* 42 (E).

Hungary. Budapest, Scti Gerardi Hill, 120M, *Degen* 231 (E).

Ireland. Cork, 19 vi 1891, *Scully* 1837 (E).

Italy. Pedemonte: Val Tournanche near Busserailles, vii 1879, *J. Ball* (E). Verona: Venetia, near Rivoli, 160-190M, 2 vii 1897, Herb. of J. Landmark s.n. (BG). Calabria: 43Km N of Catanzaro, *Davis, P. & S. Sutton*, D. 65321 (E).

Norway. S: West-Agader, Kristiansand, Odderøya, Silokaia, *Tore Øurem* 38098 (O). SE: Oslo, *Hovda* 115 (O). SW: Bergen, 1908, *Holmboe* s.n. (O). N: Tromsø, Tromsøya, Rundvannet/Stakkevollan, 160M, 5 x 1982 *Elven* s.n. (O). N: Nordland, Sør-Trøndelag, Buvik, *Lyche* 32606 (O).

Portugal. N: Bragança, Lameiros, *Pereira Coutinho* 188 (LISU).

Trás-os-Montes & Alto Douro, Mirandela, *Beliz & Ruivo* 800

(ELVE). C: Guarda, Torrião, 500-1000M, *R. Fernandes & Sousa* 3265 (COI). S: Alto Alentejo, Portel Hills, road to Oriola, Abegoaria, c. 400M, *Malato-Beliz et al.* 16607 (ELVE).

Romania. Brasov, near "Rétyi Nyir", 1911, *sine coll.* 352 (E).

Sicily. Catania: N of Nicolosi, 2500M, *Davis, D. & S. Sutton, D.* 64415 (E). Etna, v 1841, *J. Ball* s.n. (E).

Spain. Sierra de Gredos, 950M, *Deverall & Flannigan* 0151 (E).

Granada, Sierra Nevada, 3100M, *Chamberlain et al.* 258 (E).

Cuenca: Sierra de Valdeminguete, 1600-1700M, *Brummitt et al.* 595 (E). Logrono/Soria: Sierra de la Urbion, 1700M, *Dresser* 627 (E).

Sweden. Uppsala, *Hartman* 389 (O). Öland, 22 vi 1974, *Halvorsen* s.n. (O). Gotland, 26 vi 1926, *Asplund* 257 (O). Kristianstad, 10 vii 1912, *Tufvesson* s.n. (O).

Switzerland. Grimsel Alps, viii 1858, *Balfour* s.n. (E). Zermatt, viii 1905, *Brown* s.n. (E-GL). Basel, vi 1918, *Jermstad* s.n. (O).

Turkey. A₂: Istanbul: Alibey Köyü, *Aveigoil* 5848 (E).

United Kingdom. England: Suffolk, Hertford, 29 vi 1885, *Linton* 2797 (E). Wales: Aberdare, 1902, *Riddelsdell* 1837 (E). Scotland: Selkirk, 10 vi 1966, *Webster* 10571a (E); Edinburgh, Leith Docks, 20 vi 1883, *Christie* s.n. (E).

USSR. Rossya: Pskov, 18 v 1913, *Andreev* s.n. (E); Novgorod, 17 vii 1925, *Selivanova* s.n. (LE); Moskva, 30 vi 1967, *coll. illeq.* s.n. (LE). Ukraine: Kerson, *E. Pobedimova* 5109 (E); Kiev, Tarashcha, 30 vi 1916, *D. Litvinov* s.n. (E).

Yugoslavia. Sarajevo, 13 vii 1960, *Webster* 4031 (E).

N AFRICA (+ CANARY ISLANDS)

Algeria. A₁: Chréa, c. 1500M, *Davis* 59132 (E). C₁: Col de Telmet, W Batna, 1450M, *Davis* 52584 (E). H₁: Tiaret to Aflou, 1100M, *Davis* 58588 (E).

Canary Islands. Tenerife: El Portillo, 2030M, *Tore Ourem* 30637 (BG); Llano de Ucanca, 2250M, 11 III 1960, *Johannes Lid* s.n. (O). Los Azulejos, 2230M, 29 iv 1957, *Johannes Lid* s.n. (O); B'co. Riachuelo, 2050M, 28 iv 1984, *C. Rodriguez* s.n. (E-GL).

Morocco. MA: between Azrou and Timhadite, 1850M, *E. Paunero et al.* 1928-29 (E).

ASIA (+ CYPRUS)

Afghanistan. N: Baghlan: W-exposed slopes in dense *Juniperus polycarpus* stand, 2400M, *Freitag* 2707 (hb. Freitag). SW: Herat: mountain above Chesmeh Obeh, stony slopes, 2400M, *Hedge, Wendelbo & Ekberg*, W 7853 (E). SE: Zabul: Kalat-i-Ghilzai, 15Km SW, intensively grazed, dominated by dwarf *Amygdalus* semidesert, 1550M, *Freitag* 413 (hb. Freitag). E: Kapisa: Panjir-Tal, [2n=14], 2500M, *Podlech* 12811 (E). NE: Badakhshan: Anjuman Pass, 4050m, *Podlech* 12344 (E). C: Banian: Band-i-Amir, c. 2800M, *Rechinger* 18400 (W).

China. Qinghai: Huang Yan Hsien (W from Xining), in vegetable garden, *Keng* 5477 (K). Gansu: Labrang, Kan-ping-ssu, near Xining, exposed steppe, *Keng* 5750 (K); Sichuan: between Batang and Iachienlu, IX-X, 1904, *Hosie* s.n. (K).

Cyprus. Tripilos, 9 iv 1933, *Foggie* 164 (E); 1380m, 9 vi 1961, *Young* 7368 (E).

Egypt. A. *Kaiser* 783 (G); *Schimper* 175 (E-GL).



Iran. N: Azerbaijan: 47°50'E, 38°24'N, 2400M, *D. Walton* 98 (E). E of Arak, 1645M, *Archibald* 1732 (E). E: Shahrud-Bustam: Qaleh Bala, 1120M, *Rechinger* 50356 (W). C: Tehran: Tehran, taller plants from close to rock, shorter from open ground, c.1700M, *Lamond* 2783 (E). S: 42Km Kerman to Bam, 1900M, *Leónard* 6014 (BR).

Iraq. MRO: Shaqlawa, abundant, 1066M, *R. Haries* 727 (E).

Jordan. Gerash, 530M, *Meyer & Dinsmore* G 747 (E). Petra, 970M, *J. Dinsmore* 6747 (E).

Pakistan. W: Baluchistan: Ziarat, 2438M, *R.R. Stewart* 27935 (RAW). Near Quetta, common desert annual near Quetta, *R.R. Stewart* 27934 (RAW).

NW Himalaya: Chamba, Pangi, Hunan Mullah, c.3352M, 9 vii 1917, *R.R. Stewart* s.n. (RAW). Lahul, Kyelang, *Bor* 9220 (RAW). Kashmir: Astor Distr., Chillam, Gilgit road, 3048M, *R.R. Stewart* 18995 (RAW).

Syria. Jabal Druze, N of Shahba, Tell Shihan, *Barkoudah* 1263 (E). Nebk, Mar Musa, *Davis* 5542 (E).

Turkey. A5: Yozgat, Cekerek, 1250M, *Doğan* 218 (E). B9: Bitlis, Bitlis, 1550M, *Davis* 43370 (E). C5: Niğde, Hasan Dağ, 2300M, *Davis et al.* 18944 (E). C8: Mardin, Savur, 900M, *Davis & Hedge*, *D.* 28547 (E).

USSR. Armenia: Vedibassar Prov., prope Beink-Vedi, mont. Jlanln, *Schelkovnikov* 10128 (E). Erivan, Schugavit-Noragavit, *Araratian* 11627 (E). Turkmenkaya: Krasnowodsk, *Sintenis* 1585 (K). Kopet Dag mountains, 900M, *V.V. Nikitin et al.* s.n. (K). Uzbekskaya: c.70Km W Bucharra, OM, *C. Townsend* 86/104 (K).

AMERICA

Canada. Ontario: Niagara Falls, 11 vi 1891, *J. Macoun* s.n. (E).
 U.S.A. California: Tejon Pass, 1200M, *Davis & Lightowlers* 67025
 (E). Colorado: Paradox, Montrose Co., 1670M, *E. Walker* 170
 (E). Idaho: Boise, c.800M, *J. Clark* 52 (E). Maryland:
 Columbia, *A. Ruth* 880 (E). Michigan: near Port Huron, 27 vi
 1903, *C. Dodge* s.n. (E). Montana, 1066M, *Hamilton* 762 (E).
 Nevada: Nye Co., c.210M, *A. Heller* 9685 (E). N Carolina: Rowan
 County, *A. Radford* 44737 (E). Oregon: Klamath valley, *W.*
Cusick 2844 (E).

AUSTRALIA

Camberra, A.C.T.: Thredbo River, near Jindabyne, abundant as weed
 of disturbed and burnt areas near the river, *L. Adams* 1536
 (K). Victoria: Melbourne, cow market, xi 1921, *O. Brien* s.n.
 (K).

NEW ZEALAND

South Island: Cromwell Gorge, *J. Hubbard* 253380 (K).

COMMENTS

Many varieties have been described within *B. tectorum* subsp. *tectorum* as here described. The most relevant ones, or those that most frequently occur in the literature or on herbarium labels, are:

var. *nudus* Klett & Richt., Fl.Leipz. 109 (1830) and var. *glabratus* Spenner, Fl.Friburg, 1: 152 (1825) with glabrous

spikelets, as in the Linnaean type specimen;

var. *hirsutus* Regel in Act.Hort.Petrop. 7: 600 (1880); var. *genuinus* Gren. & Godr., Fl.Fr. 3: 583 (1853); var. *pubescens* Schur., Enum.Pl.Transsilv. 805 (1866) - with pubescent spikelets; and var. *longipilus* (Kum. & Sendt.) Richt., Pl.Eur. 1: 114 (1890) - with very long hairs indeed;

var. *ponticus* (C. Koch) Asch. & Graebn., Syn. Mitteleur.Fl. 2: 594 (1901) with spikelets having only one fertile floret;

var. *grandiflorus* Hack. ex Fedtsch. in Bull.Jard.Bot. Pierre Grand 14, Suppl. 2: 89 (1915) - nom.nud. - with very long spikelets.

In my opinion, varieties based on pubescence should not be recognised. In fact, indumentum varies continuously from almost absent to dense with long hairs, and this pattern of variation occurs not only in the other *Genea* species but in *Bromus* in general.

Nor do I consider varieties based on the number of fertile florets as worthy of recognition. I have observed several specimens of *B. tectorum* var. *tectorum* with only one fertile floret. Apart from the fact that they seem to be concentrated in SW Asia, there they seem to be distributed at random. It could be argued that this is a result of phenotypic plasticity in plants that grow in very poor conditions. However, I have not observed a significant reduction of floret number in the sect. *Genea* species I grew for the Phenotypic Plasticity Experiment (Chapter 4). On the other hand, some specimens of subsp. *tectorum* that grow in very poor conditions in SW Asia, sometimes growing with subsp. *lucidus*, have 3 fertile florets. Some of these single-grained

plants show very well-developed vegetative parts [e.g. "Afghanistan: N: Baghlan: N Salang, 2400M, Freitag 2707 (herb. Freitag!)]]; this is, in fact, a plastic characteristic indicative of good environmental conditions (as I have observed in the same experiment). The combined characters of lush vegetative growth and very small spikelets give a different facies to the plant, especially when young and the panicle branches are still erect. I, therefore, think it is possible that underlying this single-grained phenotype there is, at least sometimes, a real genotypic variation, but I do not think this is enough to give it formal status.

B. scabriflorus Opiz, of which I saw the type specimens that are at PR, was used to describe a plant with very small spikelets and 1 or 2 fertile florets. It is very much like the plants to which I refer above. The diagnostic features of the type specimen based on my own observations are listed below:

Leaf blade length: 4.8-13cm

Panicle length: 11cm

Longest panicle branch in the lowermost panicle node: 6.8cm

No. of nodes in the panicle branch above: 3

No. of spikelets in the panicle branch above: 6

Panicle branches pubescence: many, very short hairs

Spikelet length: 1.4cm

No. of florets per spikelet: 7 (1-2 fertile)

Vein no. on lower glume: 1

Vein no. on upper glume: 3

2nd lemma length: 10.7-11.3mm

Outline of spikelet including awns: irregular

Anther length: 0.8

Callus on rachilla at the base of each fertile floret: fully
developed

2nd awn length: 13-15.5mm

2nd palea length: 6.8-7.7mm

B. tectorum L. subsp. *lucidus* Sales, nom. nov.*

Syn.: *B. sericeus* Drobov in Fedde Rep. 21: 39 (1925), non *B. sericeus* Tenore, Fl.Nap.Prod. 1(1): X (1811-15); *B. sericeus* Drobov subsp. *fallax* H. Scholz in Willdenowia 19: 133 (1989).
Type: Sinai, auf Granitsand am Füsse des Dschebel Musa, 1500M, Kneucker 290 (B - Holo!); *B. moeszii* Pénzes, in Magyar Bot. Lapok 33:24 pl.10 (1934). Type: Iran, Auf Äker u. Strassen Gräben bei [Daulatabad] Dolitabad, Pichler 18 (G - Holo!).

Prior to the publication of Drobov's *Bromus sericeus* in 1925, there is an earlier "*Bromus sericeus*", i.e. *B. sericeus* Ten., Fl.Nap.Prod. 1(1): X (1811-15). In the second volume, pt I, of the same work, Tenore considers this *B. sericeus* Ten. a synonym of *B.*

* The formal publication of this name is currently (Feb. 1991) in press (Sales, 1991) in a paper which deals with different aspects of *Bromus tectorum* and its subspecies.

alopecurus Poiret, Voy. Barb. 2: 100 (1789). *B. alopecurus* Poiret belongs to sect. *Bromus*. The differences in panicle shape between the two descriptions are clear enough to say that these two authors were describing different taxa. Tenore's *sericeus*, based on a plant from Naples, Italy, had a narrow and condensed panicle which agrees with the description of *B. alopecurus*. Drobov's plant had loose and secund panicles. The name "*B. sericeus*" Drobov is thus a later homonym and has to be replaced by a new epithet. It seemed appropriate to adopt the name "*lucidus*" (= shining) because of the shiny or silvery appearance of the spikelets.

Icon.: Bor in Townsend & Guest, eds, Fl. Iraq 9: tab. 53 (1968).

Type: "Tashkent post. Syr Darya district, middle part of Keles basin, Kaplanbeck demarcated area, c. 1500M 4 v 1921, Abolin 7496 (TAK !). Lectotype selected by Tsvelev, *Grasses of the Soviet Union* 1, 326 (1984). Syntypes at Leningrad (LE).

Diagnostic features of the type specimen based on my own observations:

Leaf blade length: 2.8-5cm

Panicle length: 2.8-4.5cm

Longest panicle branch in the lowermost panicle node:
0.8-2.3cm

No. of nodes in the panicle branch above: 0-1

No. of spikelets in the panicle branch above: 1-2

Panicle branches pubescence: short erect hairs

Spikelet length: 2.6-2.9cm

No. of florets per spikelet: 10-11

Glume shape: ovate-oblong

Vein no. on lower glume: 3 (4,5)

Vein no. on upper glume: 7

2nd lemma length: 18.1-18.3mm

Top of spikelet including awns: irregular

Anther length: 1.2mm

Callus on rachilla at the base of each fertile floret: none or
very incomplete

2nd awn length (second fertile floret from the base):
23.2-24mm

2nd palea length: 12.2-12.5mm.

Habitats: from sea level to 1900m, generally at higher altitudes in Iran, Afghanistan and often E Mediterranean, but in lowlands in Turkey, Saudi Arabia, Iraq and Kuwait; on more or less dry silt, usually over limestone, calcareous, clay, lava, gypsum and saline soil; in compact, stony or gravelly, loose drifted or fixed sandy soil; in desert and semi-desert wadis, steppe, very rarely in wet areas (probably introduced), such as muddy gravelly river banks; hill slopes, open flat valleys, as a weed in fields, rarely in gardens; often with *Aellenia* (*Halothamnus*) *subaphylla*, *Amygdalus*, *Artemisia*, *Astragalus glaucophyllus* and *Malcolmia grandiflora*.

Selection of specimens studied (see also page 48)

ASIA (+ CYPRUS)

Afghanistan. N: Samangan: Taschkurgan, 420M, Freitag 5062 (hb. Freitag). SW: Herat; Obek, "Hot Springs" valley, 1371M, R. & E. Gibbons 506 (E). SE: Kandahar: 60Km W Kandahar, 900M, Freitag 503 (hb. Freitag).

Iran. W: Kordestan: Sanandaj, 1300M, *Jacobs* 6722 (W). E: between Dasht-e-Kavir and Dasht-e-Lut, 1250M, *Leónard* 5521 (BR). C: Semnan: SE of Shahrud, 830M, *Freitag* 15262 (hb. Freitag). S: Baluchistan: 100Km S Zahedan to Khash, 1750M, *Rechinger* 54735 (E).

Iraq. DWD: 13Km E K₃, 680M, *Rawi et al.* 32959 (K). FPF: 20Km to Khanqin, *Fanzi & Noovi* 39591 (K). LCA: Haswa, between Baghdad and Falluja, *Omar & Wedal* 47500 (K). MAM: Jarsang to Amadiya, *Kaim et al.* 41010 (K).

Jordan. Wadi Araba-Wadi Khalid (N Fenan), 350M, 9 iii 1986, *Kürschner* (E). Wadi Ram, *Davis* 9105 (E).

Kuwait. 6th Ring Road, near the Golf course, 40M, *Rawi et al.* 10936 (KT). Sobiya, by the sea shore, *Rawi & El-Kholy* 12330 (KT). Along the Salmi highway, 136Km from Rikka, 200M, *Rawi et al.* 10650 (KT).

Pakistan. W: Quetta: Sariab, 1700M, *Rechinger* 28842 (W). Khanai, *V. Parkash* 16473 (RAW).

Saudi Arabia. N: Wadi Ar-ar Project: Al-Barka, *Al-Sooqi* 3975 (RIY). Al-Harra, *Chaudhary & Al-Jouid* 10852 (E). N/C: c.30Km W of Al Majma'ah, c.700M, *Podzorski* 921 (E).

Turkey. C₇: Malatya, c.112M, *E.K. Balls* 2246 (E). C₉: Surt: Sirnak to Gizre, 610M, *Davis* 42684 (E).

USSR. Uzbekskaya: Flora Bucharica, *Neustruev* 201 (LE).

5.1.3 MORPHOLOGY

5.1.3.1. Historical

In 1925 Drobov described *B. "sericeus"* from C Asia. Although its distinctive characteristics are well-described and known, the

lack of field work in this area deprived taxonomists of a clear idea of the great morphological variation of the taxon. Drobov in his original description distinguished his new species from *B. tectorum* by the number of veins on glumes, 3 for the lower and 5/7 for the upper, and its much longer spikelets. As time went on, the field work to support the *Flora of Turkey*, *Flora Iranica*, *Flora of Iraq*, *Flora of Pakistan*, *Flora Palaestina* and more work in the Arabian Peninsula brought to the attention of taxonomists an increasing number of specimens intermediate between *B. tectorum* and *B. "sericeus"*. The delimitation between the two taxa became very unclear. The first and so far only attempt to solve this taxonomic problem was made by Scholz (1989), who described a new subspecies within *B. "sericeus"* in Sinai (subsp. *fallax* H. Scholz) that he thought could be a hybrid between *B. "sericeus"* and *B. tectorum*. Scholz drew attention to the synaptospermous condition in *B. "sericeus"* (the florets do not disarticulate in a spikelet) in contrast to the chorispermy in *B. tectorum*, the consequence of a fully developed callus on the floret base. He described subsp. *fallax* as having a spikelet size intermediate between that of *B. tectorum* and *B. "sericeus"* and an incompletely developed callus which could be interpreted as either chorispermy or synaptospermy. I have had the opportunity of studying a very large number of specimens from the whole geographical area of distribution of both taxa. I find that the type specimens of subsp. *fallax* (which I have studied closely) represent only one of many morphological variants that can be associated with *B. tectorum*/*B. "sericeus"*. In fact, other specimens that I have observed show the condition described by Scholz more clearly than his type specimens.

Table 5.1.1 gives a synopsis of the characters used in keys by some of the most experienced botanists who have worked in the area where both subspecies grow. Some of the character states overlap: e.g. number of spikelet per branch, awn length and anther size. This shows the difficulties authors have had in separating the two taxa. The number of veins on glumes was used by all of them. However, Nevski (1934), Bor (1968, 1970) and Cope (1982) were clearly aware of variation in this character. Nevski mentioned that lower glumes are "usually 3"-veined in *B. tectorum*; Bor (1970) used only the number of veins on the lower glume. Almost certainly he was aware that the number of veins on the upper one was variable and thus an unreliable character. In fact, specimens designated hitherto as *B. tectorum* can have 3, 4 and 5 veins and *B. "sericeus"* 5 and 7. Cope refers to 3 veins for the lower glume in *B. "sericeus"*, but notes that a single vein may also be found. He probably recognised that some of the most important characters (such as lemma and awn length) used to identify *B. "sericeus"* were sometimes associated with the single veined character of the lower glume - which I have also observed. As far as lemmas and awns are concerned, only Cope specified that his measurements refer to the lowermost floret. In fact, lemmas become much shorter towards the top of the rachilla but awns increase and decrease in length towards the top. Branch length is referred to only by Kreczetovich & Vvedensky (1934) in relation to *B. "sericeus"*: their "shorter spikelet" presumably implying that in *B. "sericeus"* the branches are shorter than the spikelets. I find that, however, particularly in SW Asia and the Canary Islands, subsp. *tectorum* can have shorter branches with very few spikelets. This may be due to

TABLE 5.1.1 Synopsis of the characters used in keys (from 1934-1984) of floristic works in Asia for B. tectorum subsp. tectorum (TE) and subsp. lucidus (LU).

BOR		COPE		NEVSKI		TSVELEV		KREZ. & VVED.	
Fl.Iran	Fl.Iraq	Fl.Pakistan				Grasses of		Fl.URSS	
(1970)	(1968)	(1982)	(1934)	(1976)	(1934)	Sov. Union		(1934)	
				(1984)					
TE	LU	TE	LU	TE	LU	TE	LU	TE	LU
Branches length									
No.spikelets per branch	8	2-3		(1)2-15	1-4			Lots	1-2
Lower vein no.	1	3	1	3(1)	1	3	1	3	1
Upper vein no.	3	5	3	5	3	5	3	5	5
Lemna length (mm)	9-13	18-25	10-12 (16)	20-25	10-14	18-25	8-14	15-18	
Awn length (mm)	1-1.5	1.2-2.5			lower-most	lower-most			
Anthers (mm)							0.5-1	0.8-1.5	

shorter
than
spikelet

phenotypic plasticity in places of lower humidity and higher temperatures. Nevertheless, the geographical concentration of these plants in these two areas could be the result of evolutionary tendencies and therefore, have a genetic, selective, basis.

5.1.3.2. The present analysis

In my opinion, the characters used so far by taxonomists are not sufficient to recognise 2 independent species. I extended the number of possible differentiating characters to 38, expecting to find some that were more associated with one species than the other. A selection of these characters (9), observed in a representative number of herbarium specimens (120), was made for computer analysis. As a result of these investigations, I have established my own classification of the taxa involved, as presented earlier (5.1.2), based on both an "intuitive" and a computer analysis. A total of about 1000 specimens of both taxa, and their intermediates, was examined.

INTUITIVE ANALYSIS

It is rather reluctantly that I use here the word "intuitive". I use it in the sense of "non-numerical" and wish to make it clear that much of the information on which it is based (ecology, phenotypic plasticity, morphological variation, geography, etc.) is just as "scientific" as that analysed by the computer, but difficult to express numerically.

The extended number of 38 characters were observed in herbarium specimens covering the extremes of the geographic distribution with special emphasis on SW Asia, where both taxa

TABLE 5.1.2 Characters analysed in *B. tectorum* s.l. (including both subspecies) from a wide range of herbarium material together with an evaluation. The characters considered most reliable marked with an asterisk (*) were used for computer analysis. TE - subsp. *tectorum*; LU - subsp. *lucidus*

CHARACTER		COMMENTS
Height		Plastic character in both subspecies; TE can be much taller than LU.
Culms	No.	Plastic character in both.
	Posture	Varying randomly in both.
	Pubescence	Varying randomly in both
Sheath pubescence		Varying randomly in both.
Blade	Length	Plastic character in both.
	Pubescence	Varying randomly in both.
	Furrows/ribs	Variable randomly in TE; LU tends to have flatter blade surfaces.
Ligule	Shape	Varying randomly in both.
Articulation tissue		Varying randomly in both; LU tends to have less evident articulation tissue.
Panicle	*Length	TE tends to have longer panicles
Panicle branches	Posture	Difficult to assess accurately in herbarium specimens; longer panicle branches in LU sometimes are flexuous.
	*Length	Plastic character in TE; variable in both but strong tendency for shorter ones in LU.
	Division	Plastic character.
	Pubescence	Varying randomly in both.
	Thickness	TE tends to have thinner ones, but the difference is difficult to assess.
	No. spikelets	Plastic character.
Spikelet	*Length	Tendency for longer ones in LU.
	Shape	Constant throughout.
	*No florets	fertile Little variation.
		sterile Continuous variation, but LU tends to have more sterile florets.
	TOTAL	It tends to be higher in LU.
Lower glume	*Vein no.	Strong tendency for 1 in TE and 3 in LU.
	Size	Not used as proportional to lemma length.
Upper glume	*Vein no.	Variable in both.
	Size	Not used as proportional to lemma length.
Lemma	*Length	Tendency for longer ones in LU.
	Vein no.	Constant throughout (?).
	Pubescence	Variable in both; LU tends to be far more pubescent than TE.
	Top teeth	Not used as proportional to lemma length.
Rachilla	Pubescent	Varying the same way as lemma.
	Length	Some differences in both taxa; character associated with dispersal biology; therefore very interesting but difficult to assess.
Awn	Posture	Little variation.
	*Length	Character linked to the general facies of spikelets which is slightly different in both taxa.
Palea	Veins	Continuous variation.
	Surface	Continuous variation.
	*Length	About the same as caryopsis.
Stamens	No	Constant throughout (3)
Anthers	Length	Continuous variation between both taxa. Remarkably constant in the same plant.
Caryopsis	Length	Some differences but caryopsides not always present.

occur: Portugal, Norway, Syria, Jordan, Saudi Arabia, Kuwait, S USSR, Iran, Afghanistan and Pakistan. The variation of these characters is analysed in Table 5.1.2. The phenotypic plasticity was assessed either by comparison of the morphology of specimens that grew in rather contrasting habitats or comparing the variation shown by these plants with the ones observed in the "experiment on phenotypic plasticity".

A COMPUTER ANALYSIS OF INDIVIDUALS

It was decided to define a subset of the plants in all the material studied for taximetric analysis, which covered the total geographical range. One hundred and twenty specimens, so chosen, were then scored for the 9 characters (marked with an asterisk* in Table 5.1.2) which seemed to me to offer the best means of distinguishing subsp. *tectorum* and subsp. *lucidus* and the various categories of intermediates between them.

Although the characters chosen are thus "*a priori*" weighted relative to others which might have been included, they are not weighted relative to each other. In an ordinary taximetric analysis, 60-80 characters might reasonably be incorporated, all of nominally equal, but biologically rather different, weight. I merely seek to see what a mathematical analysis makes of the distribution of 9 characters (and 4 character states) in this population of 120 individuals. It is, after all, difficult to be sure that one's own intuitive assessment of the variation clusters is reasonable, where the OTUs are scattered in a hyperspace bounded by nine dimensions! Perhaps it is more accurate to regard this exercise as arithmetical rather than taximetric. In any case

the question being asked is less: "What clusters here are recognised as such by a numerical analysis?" than: "Using these characters, does a numerical analysis produce the same clusters as I recognise intuitively, and what, if any, geographical correlation can be seen?"

Cluster analysis by the well known hierarchical method was chosen, UPGMA (unweighted pair-group method using arithmetical averages) being the strategy used. It seems to have become the favoured method among numerical taxonomists. It is described in many standard textbooks (e.g. Sneath & Sokal, 1973; Dunn & Everitt, 1982). In this method the proximity between two clusters is defined by the average of the proximities between all elements that make one and the other. A GENSTAT "Hierarchy" program was used which has these properties.

Many similarity coefficients can be used to measure the degree of similarity/dissimilarity between OTUs, each with their own properties. The widely used simple matching coefficient (S_{sm}) of Sneath & Sokal (1973):

$$S_{sm} = \frac{a + b}{p}$$

is just the ratio of the total number of matches (positive, a , and negative, b) of character states between any pair of OTUs, to the total number of characters, P . Also popular is Jaccard's coefficient:

$$S_j = \frac{a}{a + b + c}$$

It ignores matches that are "negative matches"; a useful property, for instance, to avoid absurdity when "similarity" between 2 taxa would be recognized from the lack of some feature on both, e.g. *Homo sapiens* and a sponge are similar because neither have wings. It is not relevant here. I have selected the characters and states with some deliberation and shared absences are as relevant to my questions as are shared presences.

The simple matching coefficient is used when all character states are binary: here they are not. Using the simple matching coefficient would, therefore, create distortions because a match in a 4-state character is obliged to be less common than in a binary state character. Gower (1971) modified S_{sm} to allow for this, and Gower's similarity coefficient accordingly featured in the programme chosen.

The characters, character states and 0 1 2 coding are given in Table 5.1.3.

There has been some debate among numerical taxonomists about the applicability of hierarchical cluster analysis to individuals rather than to populations of species (Sneath & Sokal, 1973, page 368). The outcome of the debate pends further research; it is hard for a biologist to sustain the idea that hierarchies cannot exist below the species level. Numerous examples of the use of individuals as OTUs are cited by Sneath & Sokal (1973).

The raw data matrix, control file and dendrogram print-out produced by the method described above are reproduced as Appendix 5.1.1. A diagrammatic version of the dendrogram print-out, annotated to show OTU identity and geographical origin, is given here as Figures 5.1.2., 5.1.3 and 5.1.4.

TABLE 5.1.3 Characters analysed for computer analysis of *B. tectorum* s.l. (including both subspecies). Nine characters were selected from those on Table 5.1.2. The intermediate range of variation (character state 1) was based on the less frequently occurring variation in both typical extremes.

TE - *B. tectorum* subsp. *tectorum*; LU - *B. tectorum* subsp. *lucidus*.

CHARACTER	CHARACTER STATE		
	Definitions		
	0 (more like TE)	1 (intermediate)	2 (more like LU)
1. Panicle length (cm)	2.3-21	2.3-8	1-8
2. Panicle branches length	larger than spikelet	same	shorter than spikelet
3. Spikelet length (cm)	1.4-1.9	2-2.5	2.6-3.5
4. No. florets	6-10	11	11-17
5. Disarticulation of spikelet	Yes	-	No
6. Lemma length (mm)	10.5-13.9	14-16	16.1-24
7. Awn length (mm)	12.1-17.4	17.5-18.5	18.6-27
8. Palea length (mm)	8.4-9.4	9.5-10.5	10.6-14
9. No. veins on lower glume	1	-	3

Interpretation of the dendrogram (Figs 5.1.2-5.1.4)

In the dendrogram 3 groups are recognised at 37.5%, each sub-divided many times, indicating a high internal variation in each group and considerable overall morphological variation among the individuals studied.

The principal taxa in group A (A_1 , A_2 , A_3) are separated at 45-50%. Some taxa of a lower order are at 55-60%. The 61 individuals included in this group are categorised in 47 "overlapping" hierarchic categories at 77%. The principal taxa in group B (B_1 and B_2) are distinguished at 50%; taxa of a lower order are at 60%; and the 35 individuals in this group are in 29 "taxa" at 82%. The principal taxa in group C (C_1 and C_2) are at 47.5% and 52.5%; the 24 individuals included in this group are distributed by 20 "taxa" at 83%. Though not identical, given the small number of characters considered, the variability within each of the taxa A, B and C is of more or less the same order.

There are no extreme outlier individuals, but individuals no. 28, 1 and 67 seem different in group A; 90 in group B seems distinctive; 20 and 24 in group C seem distinctive also.

Figures 5.1.2-5.1.4 summarize the raw data provided by the dendrogram. See also Table 5.1.4.

Groups A and C are mainly constituted of individuals that I recognise as *B. tectorum* subsp. *tectorum* and group B of *B. tectorum* subsp. *lucidus*. Subsp. *tectorum* is virtually absent from group B, while subsp. *lucidus* has very low representation in group C. In group B almost all the variants that occur in SW Asia are plants that deviate from subsp. *lucidus*, not "towards" subsp. *tectorum* but because they have higher numbers of veins on glumes

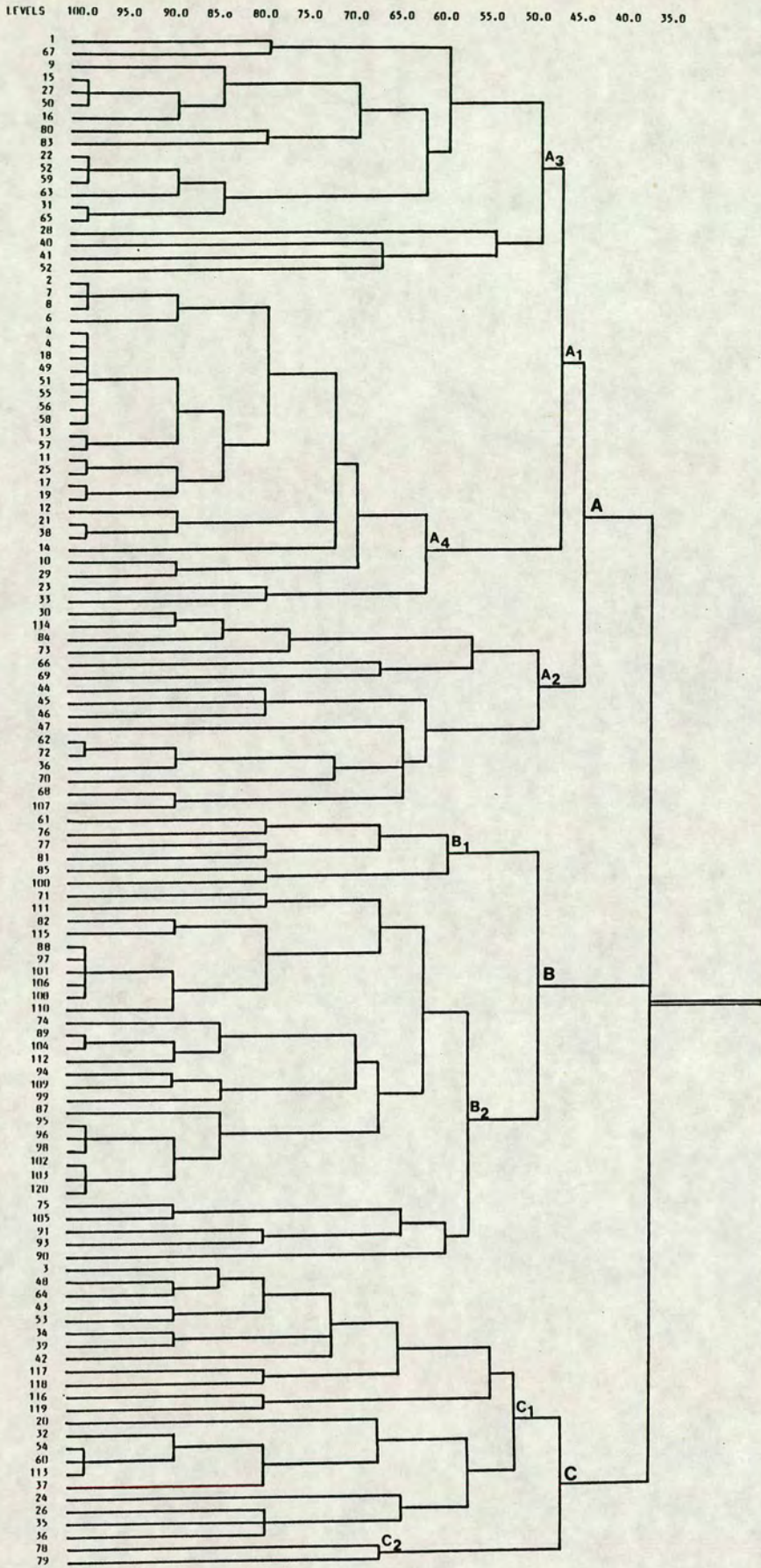


FIG.5.1.2. Diagrammatic version of the dendrogram in Appendix 5.1.1. produced by a GENSTAT "Hierarchy" programme (UPGMA method). Gower's similarity coefficient (1971) was used. Numbers identify the OTUs; in this case, single herbarium specimens.

LEVELS 100.0 95.0 90.0 85.0 80.0 75.0 70.0 65.0 60.0 55.0 50.0 45.0 40.0 35.0

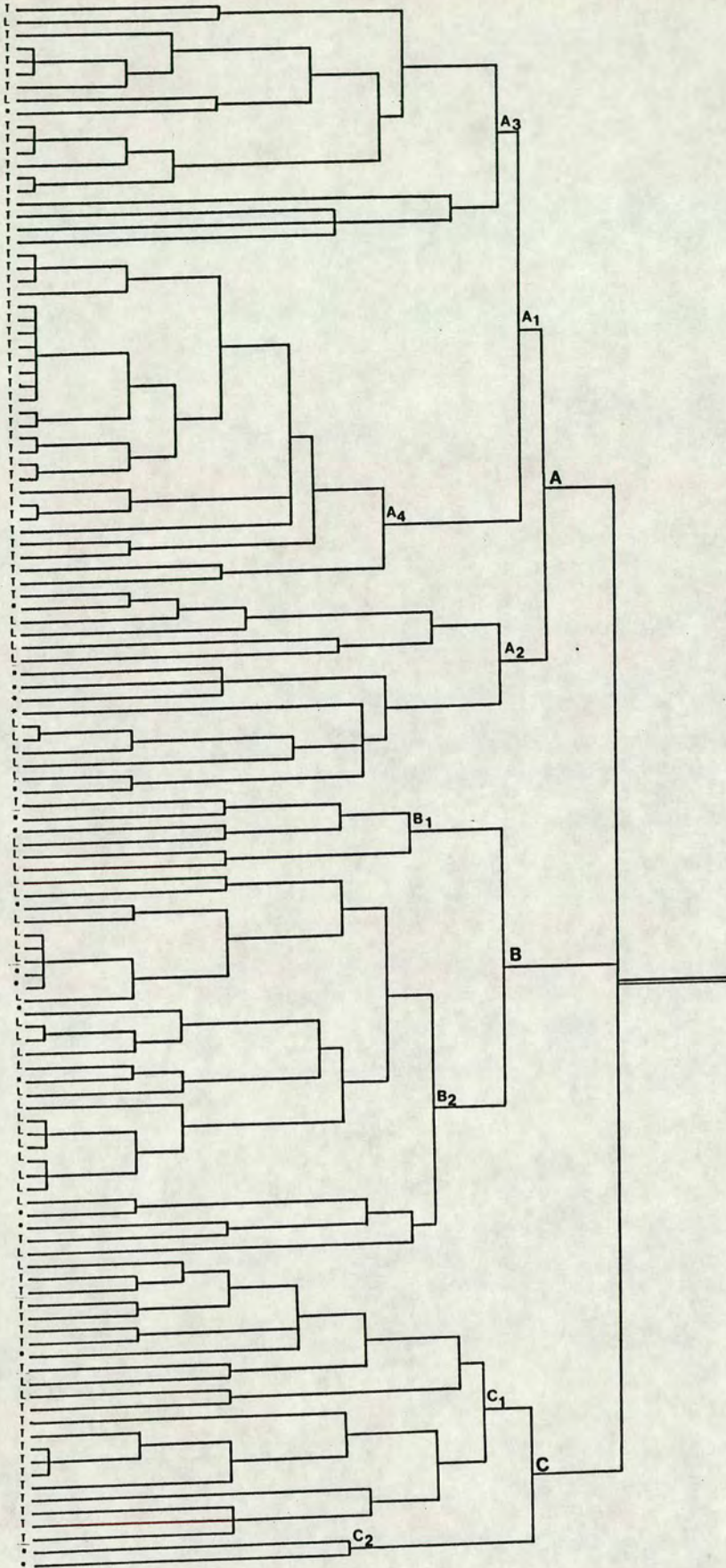


FIG. 5.1.3. Diagrammatic version of the dendrogram in Appendix 5.1.1. produced by a GENSTAT "Hierarchy" programme (UPGMA method). Gower's similarity coefficient (1971) was used. Taxonomic identification of OTUs:
T - B. tectorum subsp. tectorum; L - B. tectorum subsp. lucidus; * B. tectorum s.l. (intermediate morphologies).

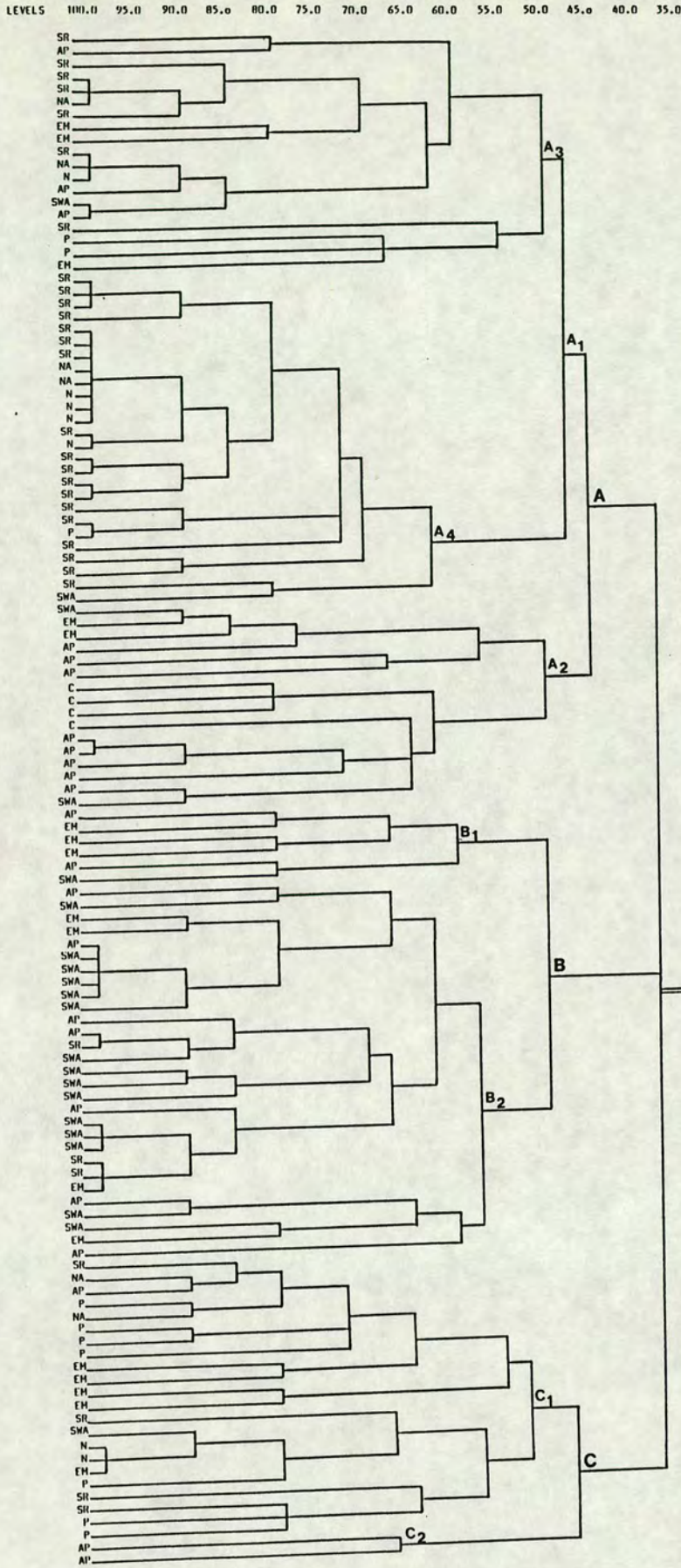


FIG. 5.1.4. Diagrammatic version of the dendrogram in Appendix 5.1.1. produced by a GENSTAT "Hierarchy" programme (UPGMA method). Gower's similarity coefficient (1971) was used. The taxonomic identification of the OTUs is given in Fig.5.1.3. and refers to *B. tectorum* subsp. *tectorum* and subsp. *lucidus*. Here the geographic origin is given: AP - Arabian peninsula; C - Canary Islands; EM - E Mediterranean; N - Norway; NA - N Africa; P - Portugal; SR - S USSR; SWA - SW Asia.

(5/7). To simplify the data, these specimens can be identified as subsp. *lucidus*. In this sense, group C seems to present an even more uniform morphology than groups A and B.

"Intermediate" morphologies are distributed throughout all 3 main groups and are concentrated in the Arabian Peninsula, E Mediterranean, SW Asia and the Canary Islands. Subsp. *lucidus* occurs only in the eastern area of distribution. Material from the Arabian Peninsula presents the highest degree of morphological diversity, being included in all 3 main groups (A, B, C) and within each group in most of the 3 main taxa here recognised (subsp. *tectorum*, subsp. *lucidus* and *B. tectorum* s.l.). E Mediterranean and SW Asia are the other areas of high variation. Material from the western area of distribution is divided between groups A and C.

The most taxonomically uniform subgroups are A₄ and B₂. The former comprises only subsp. *tectorum* and consists mainly of material from the Caucasus, the Atlas Mountains in N Africa and Norway. The second subgroup comprises subsp. *lucidus* and some specimens with intermediate morphologies between the subspecies, but mainly specimens with 5/7 veins on glumes that, as mentioned above, can be considered as belonging to subsp. *lucidus*.

Conclusions

The dendrogram clearly shows that, for the plants analysed, there is no clear-cut difference between the extreme morphologies (i.e. subsp. *tectorum* and subsp. *lucidus*), either from a morphological or geographical viewpoint. However, it points out the existence of those extremes by placing most of the subsp.

TABLE 5.1.4 An analysis of the dendrogram clusters to show (i) the percentages of specimens of the 3 "intuitive" taxa (TE = *tectorum*; LU = *lucidus*; * = intermediate) in the 3 "computer taxa" A, B and C (shown in bold), (ii) the percentage incidence of these specimens by geographical area (shown in italics). AP = Arabian Peninsula; C = Canary Islands; EM = East Mediterranean; N = Norway; NA = North Africa; P = Portugal; SR = South of USSR; SWA = South West Asia.

COMPUTER TAXA	A (61 individuals)			B (35 individuals)			C (24 individuals)			TOTAL NO. SPECIMENS
INTUITIVE TAXA	TE	LU	*	TE	LU	*	TE	LU	*	
GEOGRAPHICAL ORIGIN OF MATERIAL										
AP	3.2 8.7	26.5 39.1	-	1.6 4.3	20.6 30.4	4.3 4.3	1.6 4.3	-	8.7 8.7	23
C	-	-	17.4 100	-	-	-	-	-	-	4
EM	3.2 11.8	-	13 17.6	-	11.8 23.5	13 17.6	4.8 17.6	5.9 11.8	-	17
N	7.9 71.4	-	-	-	-	-	3.2 28.6	-	-	7
NA	6.3 66.6	-	-	-	-	-	3.2 33.6	-	-	6
P	4.8 37.5	-	-	-	-	-	7.9 62.5	-	-	8
SR	39.7 73.5	-	-	-	8.8 8.8	-	6.3 11.8	-	8.7 5.9	34
SWA	4.8 14.3	-	4.3 4.8	-	32.4 52.4	21.7 23.8	1.6 4.8	-	-	21

lucidus specimens in one group (B₂) and exclusively in the eastern area of distribution. Therefore, the dendrogram supports my view that subspecific rank is more appropriate for the taxa involved than specific rank.

The dendrogram shows a high morphological variation in the eastern area, with specimens from there distributed throughout the 3 main groups, but it shows also some variation in the west. In group A₂ intermediate specimens from the Canary Islands are placed together with subsp. *lucidus* from Arabian Peninsula pointing out the existence of E-W disjunction of the morphologically intermediate specimens. The dendrogram also supports my contention that this disjunction is due to parallel evolution. If the western plants that show intermediate features (between the subspecies) were relictual, it would be reasonable to expect that these plants would be more concentrated in one of the main groups, and not scattered as they are in the diagram. In addition, if in the west a form of subsp. *lucidus* were relictual, one might expect to find at least a few specimens with its typical morphology; especially in the course of my present comprehensive study.

In the future, the raw data on this group could be analysed by Principal Component Analysis (PCA) to determine which of the characters account for most variation and to produce "scatter" diagrams.

5.1.3.3. NOTES ON PARTICULAR FEATURES

GLUMES

The number of veins on the glumes in sect. *Genea* has traditionally been considered to be 1 for the lower and 3 for the

upper with an exception for *B. "sericeus"* with 3 and 5(7) respectively (Table 5.1.1). In the plants of *B. tectorum* and *B. "sericeus"* I find that this number varies not only from plant to plant, but even in the same plant! The upper glume can have 3, 4, 5 and even 7 veins which are associated with a less variable number of veins on the lower one. The most common combinations are 1/3, 1/4, 1/5 and 3/5, but 3/3, 3/4, 3/7 and 2/3 were also encountered. The increasing variation is not necessarily associated with the width of the glumes (i.e. not a dependent variable), as could be the case. The nervation of the lower glume seems to be a much more conservative character and therefore more useful taxonomic tool than the nervation of the upper one. The set 1/3 veins clearly predominates in Europe and N Africa and is associated with more *B. tectorum*-like typical features. I found an increasing number of veins primarily in SW Asia as already reported, but in addition and for the first time, I have observed the same in the Iberian Peninsula and Canary Islands (with a higher incidence in the latter). In SW Asia this increasing number of veins is associated most often with typical *B. "sericeus"* characters, but also with plants which have, in other aspects, an intermediate morphology, or even with typical *tectorum* characters. In the western extremity of its range this increasing number of veins is associated with *tectorum* features and in the Canary Islands with the intermediate morphologies. It seems that similar patterns of evolution may have occurred in both extremities of the overall geographical range. The higher number of veins on glumes [3/7] is sometimes associated in the eastern area of distribution (mainly Afghanistan) with ovate glumes.

The section *Bromus*, the other group of annual bromes was defined (Smith, 1970) by, amongst other features, ovate glumes, the upper one 7-veined. As I see it now, these findings about *tectorum* and "sericeus" call into question not only the present definition of both sections *Genea* and *Bromus* but even their taxonomic status. Perhaps they are less distinct than has been thought. This problem requires a deeper study on the peripheral species of each section. Special emphasis needs to be paid to the *B. pectinatus* complex, a group of plants which appear to be intermediate between both sections. This problem is discussed elsewhere (Chapter 5.1.5).

SYNAPTOSPERMY AND CHORISPERMY

Murbeck, who coined the term synaptospermy (1920), discussed the phenomenon in plants from what we now call the Saharo-Sindian region. In a long list of plants that present this condition he mentioned some grasses, e.g. *Aegilops ovata* L., *Hordeum delileanum* (Schult.) Hack., *Pennisetum ciliaris* (L.) Link - but not *Bromus*.

Synaptospermy, the condition where diaspores are released while physically attached to each other, was mentioned for the first time in *Bromus* by Scholz (1978), in particular for *B. "sericeus"*, but was never taken into account in Floras. In contrast to synaptospermy, Scholz uses the term heterodiaspory. Heterodiaspory describes the situation where diaspores have more than one form, as it is the case in *B. tectorum*. In fact, the term is not a contrast to "synaptospermy". Therefore, I use here the new term "chorispermy" (cf. van der Pijl, 1982, for a wider discussion of terms used in plant dispersal).

A chorispermous condition (Figs 6.2.33-35) exists when florets

in a single spikelet separate from each other at maturity being dispersed individually. This occurs partially for example in *B. tectorum* subsp. *tectorum*. In this taxon all fertile florets are released separately, but the sterile ones are dispersed altogether with the uppermost fertile floret (Figs. 6.2.36;37). Synaptospermy is the opposite condition (Figs 6.2.38-40). Florets remain together and are dispersed as one single unit. For the florets to separate it is necessary that the rachilla axis that holds all florets breaks below each one. For this, a callus, as a ring around this axis, needs to develop. However, mainly in SW Asia, but sometimes in the most western area of distribution, a variably incomplete callus can be found between fertile florets, thus making it sometimes difficult to decide whether a given plant is chorispermous or synaptospermous.

A false synaptospermous condition exists when there is only one fertile floret because the sterile ones disperse with the single fertile one.

In a true synaptospermous condition a question of caryopsis viability arises. Do all the grains germinate? I have observed a few herbarium specimens that grew in xeric places in which, because of the short life cycle of the plants combined with a slow rate of decomposition due to aridity, the "mother" spikelet, from which the plants germinated, has been preserved intact.

The adult plant had germinated from the lowermost fertile grain and there was no sign of germination on the other ones. The synaptospermous condition is, in fact, associated with the *B. "sericeus"*-kind of morphology - that means, in this particular

instance with plants more related to semi-xeric areas. There is a concentration of synaptospermous plants in this group in SW Asia. This example can be added to the list of Saharo-Sindian synaptospermous plants cited by Murbeck (1920).

Dispersal biology seems to play a role in speciation in sect. *Genea* where different groups of taxa present clearly different strategies. In *B. tectorum* s.l. the whole assemblage of sterile florets and its 3-dimensional arrangement for wind-dispersal, together with synaptospermy, presents a very particular and almost unique example in sect. *Genea*. Therefore it has high taxonomic relevance.

There is strong correlation between the dual character states "lower glume 1-veined/chorispermy" and "lower glume 3-veined/synaptospermy" and geographic distribution. The latter vein type is confined to SW Asia and the first is distributed through the total range of the group except for Saudi Arabia, S and SW Iraq and southern parts of the E Mediterranean countries.

Two taxonomic groups can in this way be separated. However, the existence of numerous intermediates between extremes and the fact that some odd specimens in SW Asia are still not covered by these criteria lowers the appropriate rank from the specific, as so far considered, down to subspecific level. *B. tectorum* subsp. *tectorum* must designate chorispermous plants with the lower glume 1-veined, and *B. tectorum* subsp. *lucidus* synaptospermous plants with the lower glume 3-veined.

It might be argued that the great morphological variability of these plants is due to phenotypic plasticity rather than to genetic diversity, thus further weakening not only the case for

specific rank but also possibly that for subspecific rank. However, though it is true that these plants show strong phenotypic plasticity, this manifests itself largely in vegetative parts; the reproductive ones affected are only those of panicle size and the number of spikelets (as observed during the phenotypic plasticity experiment). The reproductive characters here used to separate the two subspecies are thus certainly the expression of the genetic diversity of these plants. They are not phenotypic and they are not due to arrested development. In fact, morphological diversity in *Genea* is maintained even when plants grow in the same conditions. In two particular herbarium sheets that I have studied, both including several plants in the same gathering, one includes clear-cut examples of both subspecies, the other one includes subsp. *tectorum* and other plants with an intermediate morphology that cannot be included in one or other of the subspecies. Because such plants grow together there is a strong possibility of hybridisation between the 2 subspecies which, if it were proven, would support the taxonomic treatment here proposed.

Even with this taxonomic treatment I found plants with character states so much in between both subspecies that it is impossible to associate them with confidence to one or the other. These intermediate taxa can be grouped in the following way (see Fig. 5.1.5 and Table 5.1.5):

1. Plants that in general look like typical subsp. *tectorum* but have either 3/4 or 3/5 veins or are synaptospermous;

FIG.5.1.5 Distribution of the morphological variants of
B. tectorum s.l.:

- - General subsp. *tectorum* facies but lower glume 3-veined;
- - General subsp. *tectorum* facies but synaptospermous;
- - General subsp. *lucidus* facies but lower glume 1-veined;
- ▽ - Glumes 1/3 or 3/5-veined and callus almost completely formed;
- 7 - General subsp. *lucidus* facies but ovate-oblong glumes;
- V - General subsp. *lucidus* facies but upper glume 7-veined.

All the plant material mapped was studied.



FIG. 5.1.5. Distribution of the morphological variants of *B. tectorum* s.l.

TABLE 5.1.5 Number of specimens of *B. tectorum* subsp. *tectorum* and *lucidus* studied and mapped together with percentages of each. The morphological variants are also indicated.

Morphological variants of subsp. <i>tectorum</i> and <i>lucidus</i>								
	subsp. <i>tectorum</i>	subsp. <i>lucidus</i>	■	□	7	V	●/▽	TOTAL
No. of specimens studied and mapped	685	131	40	10	8	8	37	919
%	74.5	14.3	4.4	1.1	0.9	0.9	4	100

- - General subsp. *tectorum* facies but lower glume 3-veined;
- - General subsp. *tectorum* facies but synaptospermous;
- - General subsp. *lucidus* facies but lower glume 1-veined;
- ▽ - Glumes 1/3 or 3/5-veined and callus almost completely formed;
- 7 - General subsp. *lucidus* facies but ovate-oblong glumes;
- V - General subsp. *lucidus* facies but upper glume 7-veined.

2. Plants that in general look like typical subsp. *lucidus* but have $1/3$ veins;
3. Plants either with glumes $1/3$ or $3/5$ -veined and callus not completely formed;
4. Plants that in general look like subsp. *lucidus* but have ovate-oblong glumes. (Although this is an infrequent variant this is the morphology of the holotype of B. "sericeus");
5. Plants that in general look like subsp. *lucidus* but have $3-5/7$ veins. (Although this is an infrequent variant this is the morphology of the holotype of B. "sericeus").

These variants grow along a strip from the western to the eastern boundary, not expanding northwards (see Fig. 5.1.5). Typical subsp. *tectorum* with glumes $3/5$ -veined is the only variant that spreads throughout this geographic range being furthermore the most common one. All the others are distributed only from E Turkey and Sinai eastwards. Plants with ovate glumes and upper glume 7-veined grow exclusively in the most eastern area of distribution in Afghanistan; apart from two exceptions in E Iraq and one in E Iran.

The area of greatest morphological diversity is from the E Mediterranean Coast to NE Iran and this is probably the centre of origin of this group both according to Webb's criteria (1985) and my own conclusions.

Variant types 1, 2 and 3 present intermediate morphology between subsp. *tectorum* and subsp. *lucidus* and may support again the possibility of hybridisation between them. Variants 3 and 4, although in most ways resembling subsp. *lucidus*, present some

characters that are not even of sect. *Genea* as it has been defined hitherto. In fact, annuals with the upper glume 7-veined and the glumes ovate are characteristic of sect. *Bromus*.

It is interesting that the lower glume 3-veined is always a character associated with synaptospermy in sect. *Genea*. Table 5.1.5 gives the proportions of both subspecies and intermediates. The low percentage of the latter shows that the taxonomic treatment here proposed is reasonable.

5.1.3.4. A phytogeographical note

As a result of my analysis of such a large number of specimens (total c. 1000) throughout the total area of distribution, it is unlikely that other variants will be found. These variants seem to be more related to areas where the environmental pressures are greater in terms of temperature and humidity, as in SW Asia, and therefore where speciation is likely to be occurring at a higher than average rate. In these areas are often found not only the most highly evolved stage of this process, i.e. the subsp. *lucidus*, but different evolutionary stages from subsp. *tectorum* to it. The concentration in the E Mediterranean area is noteworthy, although it must be borne in mind that this apparent concentration may be linked with a greater number of specimens studied from this area. The occurrence of some of these stages in SW Europe, Canary Islands and N Africa showing that a similar evolutionary process is going on in the western areas but not in between, is another example of floristic disjunction between SW Asia and this area. Other examples of this disjunction are known in many plant families:

Ferula tingitana L. (Umbelliferae) found in the Iberian

Peninsula, NW Africa, Cyrenaica, SW Turkey and E Mediterranean; *Cupressus sempervirens* L. var. *horizontalis* (Cupressaceae) in NW Africa, Cyrenaica, Greece, Aegean, E Mediterranean and N Iran; *Salvia phlomoides* Asso (Labiatae) in Spain, Morocco, Algeria and Tunisia with two closely related species, *S. hypargeia* Fisch. & Meyer in C. Anatolia and *S. montbretii* Benth. in Turkish Mesopotamia, N Syria and N Iraq. A further very striking example is provided by the curious *Microcnemum coralloides* (Loscos & Pardo) Font Quer (Chenopodiaceae) in C and E Spain, C Turkey and N Iran.

Nevertheless, despite the similar patterns of geographical disjunction of *B. tectorum* and those given above, their origins must be rather different. The non-*Bromus* disjunctions here referred to are probably the remains of more continuous areas of distribution that have contracted because of increasing aridity in the E Mediterranean, as Davis & Hedge have suggested (1971). In my opinion the disjunction in *B. tectorum* must be, on the contrary, the result of adaptive radiation to somewhat similar environmental changes that are occurring both in SW Asia and the western area of its distribution.

5.1.4. GEOGRAPHY AND ECOLOGY

B. tectorum s.l. occurs in a wide range of habitats and altitudes, extending in the Old World continuously through several phytogeographical regions (as defined by Takhtajan, 1969): W Euro-Siberian, part of Macaronesian, Mediterranean, Irano-Turanian and parts of the Saharo-Sindian (Fig. 5.1.6). Subsp. *tectorum* is introduced elsewhere, concentrating mainly in areas of

Mediterranean climate in N America and Australia, failing however to colonize S Africa, but succeeding, to some extent, in New Zealand (Fig. 5.1.1). The subsp. *lucidus* has a comparatively very reduced distribution, occurring only in SW Asia (Fig. 5.1.6).

I am not absolutely certain of the distribution of subsp. *tectorum* in USSR. It is difficult to get collections from this area and often localities are illegibly hand-written and/or impossible to trace. With the material I have assembled I would say that it occurs in the south of USSR from the Ukraine to the Himalayas (Fig. 5.1.6); being rare, probably introduced, elsewhere. Tsvelev (1984) and Krecztovich & Vvedensky (1934) gave a distribution of this taxon which seems to be somewhat more extended, but basically the same as the one here presented. Apart from this area I found subsp. *tectorum* in Asia along the N boundary of the Gobi desert and E Himalayas. Especially the first of these is such an inhospitable area that certainly it is native there.

European collections are fewer than one would expect and date mostly from the beginning of this century. This might not indicate rarity but rather a reduction in the level of the recent plant collecting.

Although the herbarium at Montpellier (MPU) failed to send its important N African collections, I can understand, from the specimens studied, that subsp. *tectorum* must be restricted to the NW mountainous areas (Fig. 5.1.6). Maire & Weiller (1955) gives the same kind of distribution but also mentioning that *B. "tectorum"* grows in the very south of Algeria in C Sahara in the isolated Hoggar mountains (highest peak 2918M). Apparently this subspecies does not grow in the Tibesti mountains in S Libya (C

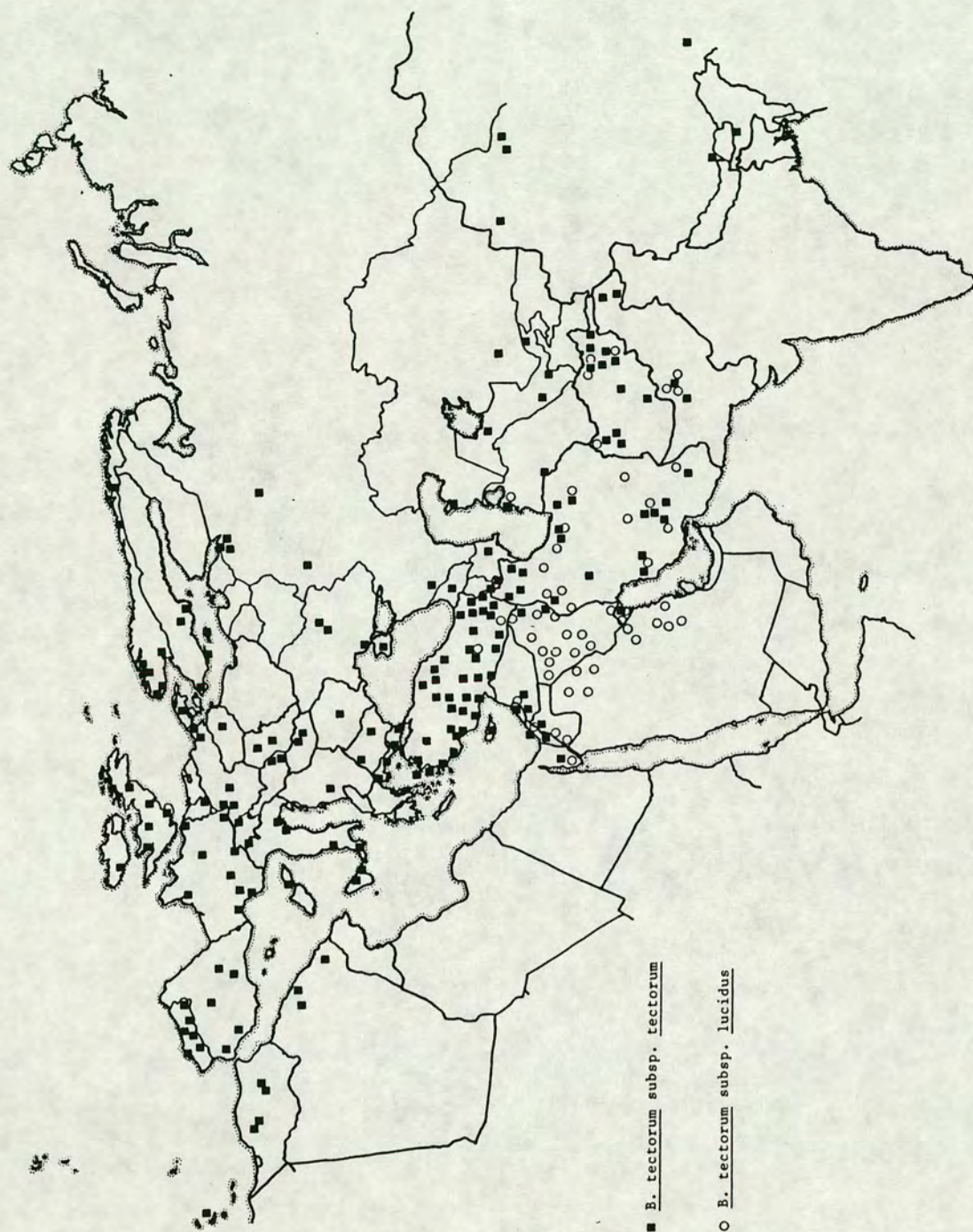


FIG. 5.1.6. Distributions of the 2 subspecies of B. tectorum in Europe, N Africa and Asia.

All the plant material mapped was studied.

Sahara) or at least has not been recorded from there.

By far the best collection of *B. tectorum* material assembled is from SW Asia. In general, the specimens have been collected over the last 50 years and often labels have some field notes on altitude, kind of soil, size of population and plant association. This contribution is particularly useful in the area where both subspecies co-exist as it is possible to point out some differences on environmental requirements. Subsp. *lucidus* does not grow, in general, at such high altitudes as subsp. *tectorum*, but the latter can grow at the same low altitudes as subsp. *lucidus* (Fig. 5.1.7). Nikiforova (1968) mentions a record of *B. "sericeus"* in the Pamir mountains up to 3800M on the lowermost gentle part of the slopes. This could be a misidentification but "this territory is very dry and quite a number of desert species are distributed there as high mountain plants; there are elevations only starting at 3700M" (Pimenov, *in litt.* 1990). Subsp. *tectorum* has strong Irano-Turanian connections and subsp. *lucidus* has developed adaptations to an especially arid environment. The latter grows in the deserts of N Saudi Arabia, SW Iraq, but does not seem to have colonized the two big deserts in Iran, Dasht-e-Kavir in the north and Dasht-e-Lut in the south, nor the deserts in S Afghanistan. However, the difficulty of collecting in these areas may be one of the reasons for the total lack of material from there. Subsp. *tectorum* can grow side by side with subsp. *lucidus* [e.g. Iran. S: Baluchistan, Bazman, 1700-2000M, *Rechinger* 55118 (W)] but in the same general area they tend to occupy different ecological and geographical niches: subsp. *tectorum* in higher, cooler, sometimes shady places, gravelly soil and higher humidity; subsp. *lucidus* in lower lands, higher temperatures, sandy soil and lower humidity.

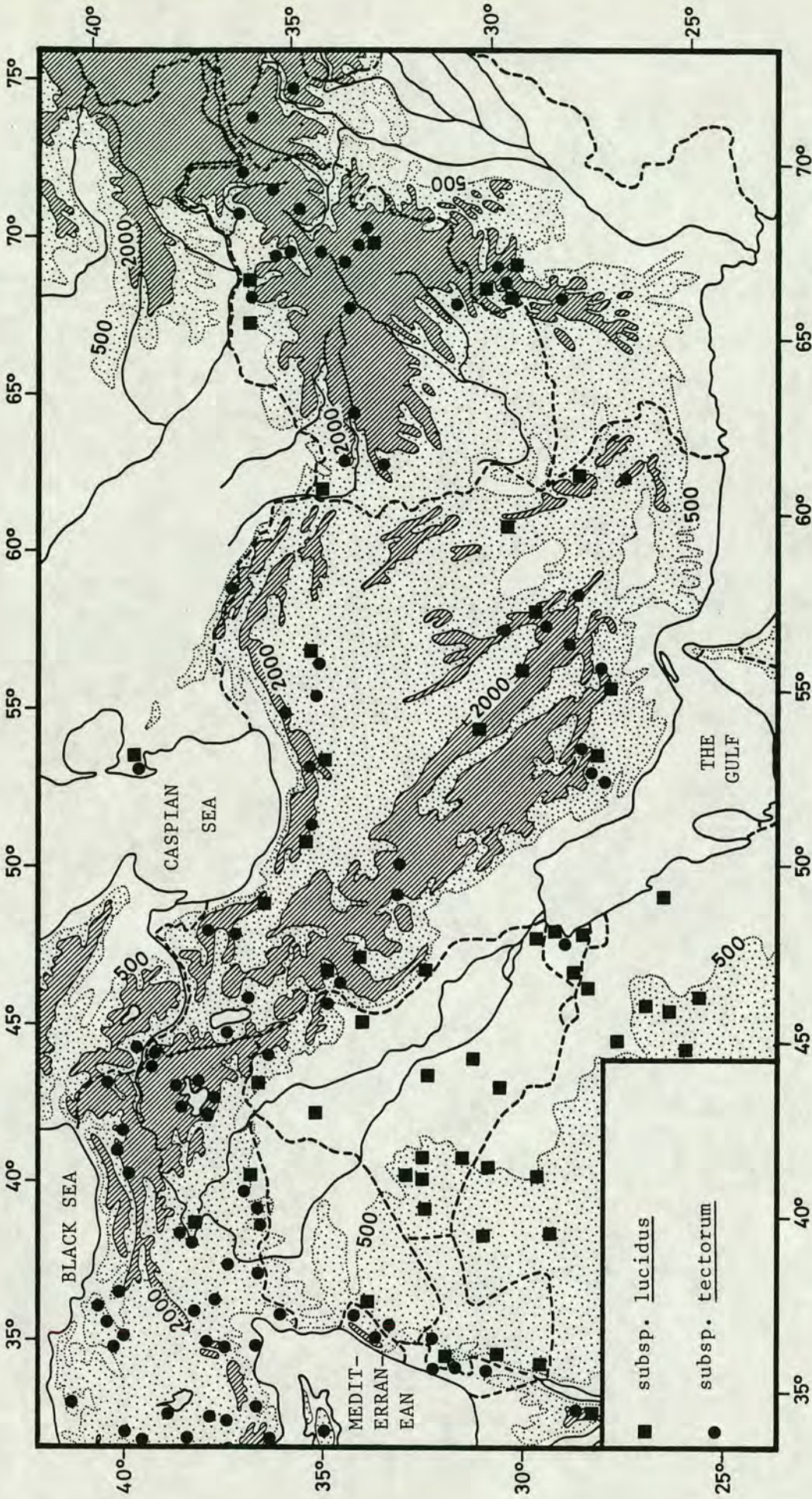


FIG. 5.1.7. Distribution of *B. tectorum* subsp. *tectorum* and subsp. *lucidus* in SW Asia; land over 500M is stippled, over 2000M shaded. All the plant material mapped was studied.

The intermediate morphologies that are more *tectorum*-like tend to occupy a *tectorum* kind of habitat; the ones more *lucidus*-like, a *lucidus* kind of habitats. The gradual transition in ecological requirements of plants that are more typical *tectorum* to clearly distinct *lucidus* supports the idea here explained that *lucidus* is in the process of emerging as a species from *tectorum* but as yet the separation is not complete. Hybridisation, if it occurs, would delay but not, in the end, frustrate such a process if the selection pressures are consistent.

In C Europe the gatherings are scarce and in the north they are never far away from the coast-line, e.g. N France, N Germany, Denmark, SW Ireland (apparently recorded for the first time), U.K. and Scandinavia. The type subspecies has been introduced into various parts of Britain and the rest of N Europe. It is of interest to note that recently subsp. *tectorum* was found even in the very N of Norway at c. 70°N!. Wendelbo (1956) mentioned its distribution in Norway totally linked with man ("anthropochorous" species). In Scotland it is a very rare roadside weed.

In Portugal, where I have some field experience, subsp. *tectorum* is quite a rare plant that grows inland in areas of more continental climate with cooler winters and sometimes snow and away from the milder Atlantic influences; the two herbarium specimens I have observed from near the coast are certainly introduced. One is from Lisboa and the other from Coimbra.

Although subsp. *tectorum* is distributed throughout the South of Europe it seems to have a rather discontinuous distribution there occupying the cooler mountain areas and occasionally low lands near the sea. The Euro-Siberian characteristics of subsp.

tectorum might have originated during periods of glaciation. When temperatures rose after the last glaciation, this subspecies, maintaining its Euro-Siberian characteristics, invaded, naturally or with man or his animals, the milder valleys and cooler, more humid places northwards. If Maire's reference to subsp. *tectorum* in the Hoggar Mountains (C Sahara) is correct, then these populations are certainly relicts of glacial times when the boreal flora moved southwards.

N America

Subsp. *tectorum* seems to have been introduced in N America at least as far back as the middle of last century, the first reference to it being from Pennsylvania in Alphonso Wood's *Classbook of Botany* (1861). The first collections from western USA date from 1894 in Utah (coll. Marcus E. Jones) and 1895 in Colorado (coll. C.S. Crandall). The oldest herbarium specimen of this taxon I have observed dates from 1891 and was collected at the Niagara Falls [Canada, Ontario: Niagara Falls, 11 vi 1891, Macoun]. A more detailed account of the spread and distribution of the species in the Ontario region is given by Dore & McNeill (1980). Subsp. *tectorum* is spread throughout most of USA, except SE (Fig. 5.1.1). It is an aggressive introduced winter annual that is well established over millions of hectares in western N America especially in the Intermountain area (Klemmedson & Smith, 1964). Although its slow growth in spring and short green feed period (when the temperature rises the plant can finish its life cycle in 6 weeks), the large populations produce large amounts of leaf area, making it a useful source of forage. Nevertheless, these

plants are an undesirable weed that is gradually replacing the local flora in some places. It is also a fire hazard in the end of its life cycle. Grains of *B. tectorum* often survive high temperatures thus explaining the rapid domination of sites after fires (Klemmedson & Smith, 1964). Many research papers have been published dealing with the control of *B. tectorum* in W America, e.g. Cline *et al.* (1977), Young *et al.* (1976), Hull & Hansen (1974), Evans & Young (1977).

The specimens I have observed occur between 750-2450M and the herbarium labels often indicate that they usually grow in disturbed or waste areas, along railways and roadsides.

S America

B. tectorum is recorded from Uruguay (Rosegurt *et al.*, 1970) and from Argentina (Nicora & Rugulode Agrazar, 1987) but I have not seen specimens from these 2 countries.

Hawaii

B. tectorum is recorded from Hawaii (Rotar, 1968); I have not seen specimens.

Australia and New Zealand

Subsp. *tectorum* grows in these two countries, but seems to be very rare there (Fig. 5.1.1). I found very few herbarium specimens and the bibliography very rarely refers to it. The information on the labels of the specimens observed, and cited above in the citations of this taxon, suggests that subsp. *tectorum* might follow the same pattern of invasion as in USA.

5.1.5. SUBSP. *TECTORUM* AND SUBSP. *LUCIDUS* AND THEIR RELATIONSHIP TO *B. PECTINATUS* AND ITS ALLIES

Together subsps. *tectorum* and *lucidus* occupy a rather interesting position not only from a morphological, but also from an evolutionary viewpoint. Within sect. *Genea* they constitute a rather separate unit with particular dispersal strategies. At the same time, they deviate somewhat from the conventional idea, or description, of the section, presenting clear morphological and geographical affinities with the *B. pectinatus* complex of sect. *Bromus*. How the *B. pectinatus* complex relates to sect. *Genea* is not yet fully understood but the link seems to be via *B. tectorum* s.l. Both subspecies and this other complex form a misty boundary between sect. *Bromus* and sect. *Genea* questioning the taxonomic reality of the these sections.

In this study I have not gone deeply into the *B. pectinatus* complex - which is poorly known. It is on the fringe of the thesis topic. However, I went deep enough to understand that the differences between this complex and the *tectorum/lucidus* group are often subtle and more quantitative than qualitative - a fact that has not previously been sufficiently emphasised.

The *B. pectinatus* complex, as described by Scholz (1981^a), includes the following species:

B. pectinatus Thunb., described from S Africa*[overleaf]

B. pulchellus Figari & De Notaris, described from Sinai;

B. rechingeri Meld., described from Afghanistan;

B. gedrosianus Péntzes, described from Pakistan, Baluchistan

B. tibetanus H. Scholz, described from India, Ladakh;

B. pseudojaponicus H. Scholz, described from Afghanistan.

The fact that the *pectinatus* complex grows in the area of highest diversity of *B. tectorum* s.l. (SW Asia) and because in the past both groups were poorly known it is understandable that some of the *pectinatus* complex specimens have been confused with *B. tectorum* s.l.** In particular, this has been the case with *B. pulchellus* in Sinai and the Arabian Peninsula. I have seen several herbarium specimens wrongly identified as *B. tectorum* (e.g. "Sinai, v 1849 Figari s.n. (E)" and "Saudi Arabia: Baha Camp 41' 24' E, 20' 9' N, 2100M, 1983, K. Smith KGSBC8 (K)"). The striking superficial similarities (similar habit and panicle shape, flexuous, nodding panicle branches, spikelets of similar size with several sterile florets) are in contrast to the far more important differences, which basically concern the spikelet structure. In true *B. pulchellus* 4 fertile florets are separated by short

* This species occurs as well in tropical E Africa mountains (2000-3000M as ruderal) and in SW Asia; there are many examples of this kind of distribution in other plant families.

** At the other extreme of the morphological facies, *B. pectinatus* type plants are often confused with *B. japonicus* Thunb., a diploid species of sect. *Bromus*.

rachilla segments with a full callus developed at the base of each one; the sterile florets are usually 3 in number and are so small and their rachilla segments so short that they are fully or almost fully enclosed in the fertile ones, giving a particular truncated look to the spikelets at maturity and contributing to a width/length ratio greater than in *B. tectorum* s.l. This arrangement of sterile florets can be found in other species of *Bromus* than in sect *Genea*. The awns, erect but not totally straight initially, are recurved outwards at maturity. There are minor differences in the shape of glumes and lemmas which are indistinctly lanceolate in *B. pulchellus*.

The most characteristic specimens of subsp. *tectorum*, with their long, nodding panicle branches, somewhat irregular awn outline, present, as far as macromorphology can reveal, a closer relation with the *pectinatus* complex than the most typical specimens of subsp. *lucidus*. The latter, with its unique, more contracted panicles, synaptospermy and the awn tips at the same level, indicate a separate evolutionary tendency departing from the older block of species to which subsp. *tectorum* and the *pectinatus* complex seem to belong.

The higher number of veins on glumes in subsp. *lucidus* (as in *B. pectinatus* complex) in relation to subsp. *tectorum* remains, however, a puzzling evolutionary tendency. Higher numbers of veins can be regarded as a primitive character since the highest numbers can be found in the perennial brome grasses (sect. *Ceratochloa* with 3-5 nerves on lower glume and 5-7 on the upper). Annuals tend to have a smaller number of veins, especially reduced in most of sect. *Genea* species, which seems to be a very recent group. If

subsp. *lucidus* is a taxon in the process of speciation, as has been argued above, it would be expected not to have such a high number of veins on glumes. This fact may be related to the biology of these plants. A larger photosynthetic area and a higher number of veins on reproductive structures (e.g. lemmas and paleas) may represent a significant adaptation when the vegetative photosynthetic surfaces are not functional towards the end of the life cycle which is very short in *lucidus* (Fig. 5.1.4). Thus it may be that the general reduction in vein numbers has here gone into reverse, associated with the transference of photosynthetic function to the spikelet. As pointed out by Smith (in ed.) even awns frequently have a photosynthetic function in annual grasses and I have observed possible functional stomata in the awns of these grasses.

AND

5.1.6. EVOLUTION/ADAPTIVE RADIATION

As previously stated, subsp. *tectorum* and *lucidus* typically occupy different habitats. The former is more an Euro-Siberian and Mediterranean plant of high places while the latter is typically a plant of dry and hot low lands. In SW Asia, both subspecies occur in areas of Irano-Turanian vegetation. The Euro-Siberian climate is characterized by long, cold and wet winters. In the places where subsp. *lucidus* grows the climate is xeric or semi-xeric. Long periods of drought are followed by short spells of rain and their sandy/gravelly soils quickly drain away the water. The Euro-Siberian region has been subjected to major environmental changes during Pleistocene due to the glaciations, while the Saharo-Sindian region has expanded dramatically in recent times

with deserts invading the Irano-Turanian areas. Mountains offer far more diverse kinds of habitats, as well as more changeable ones, than low land xeric areas. In the former kind of habitat, selection for efficient dispersal, so that plants remain in contact with their niches, is thus a vital desideratum. In this connection subsp. *tectorum* often produces big panicles and large number of spikelets; the grains are light, disperse separately and the awns are straight, outcurved. Dispersal is effected (probably for the most part) by grazing animals common in these areas.

In SW Asia the expansion of xeric habitats is pressurizing these plants and promoting adaptation and evolution. Different stages of this on-going process in the *tectorum* group are recognizable and common. The most advanced stage is here regarded as subsp. *lucidus*. The increasing aridity and irregular periods of rainfall, therefore the short growth season, promote the selection of vigorous seedlings and bigger grains. The bigger the grain the less dependent is the seedling initially on its environment. It provides enough nutrients for the formation of a well-developed root system able to absorb as much as possible of the little moisture available without being handicapped by well-developed vegetative photosynthetic parts that would lose water by transpiration. However, the formation of big grains takes energy and time and both are precious when the life cycle is very short. For this reason, fewer spikelets and fewer grains per spikelet are produced in subsp. *lucidus* as well as smaller panicles than the type subspecies. All the florets are released together with the lowermost, the only one to germinate, to provide protection against desiccation. For seed dispersal these plants

cannot rely on animals in such inhospitable areas, but depend on wind dispersal. The large number of sterile florets, released together with the only one that germinates, enlarges the surface of resistance to wind, being easily carried by it. This extra structure in relation to subsp. *tectorum* does not imply a higher input on reproduction because the total number of grains is smaller. Furthermore, the extra surface does not bring an extra loss of water due to evapo-transpiration because most of this area is typically non-photosynthetic hyaline tissue (I have not observed any stomata in this area - Fig. 6.2.9). Loss of water is further avoided by a better developed hairiness on the structures that remain photosynthetic until the end of the life cycle (reproductive parts: glumes, lemmas and rachilla).

According to Scholz (1978), the sterile florets in subsp. *lucidus* have a role to play in burrowing the grains into the soil: the top segments of the rachilla performing twisting movements of a hygroscopic nature making the sterile lemmas spread out and eventually forcing the spikelets to penetrate the soil. I have noticed that the rachilla segments in both subspecies are initially straight, but towards the end of the life cycle they are twisted. If Scholz's interpretation of this morphology is correct, then even subsp. *tectorum* "adopted" this strategy to bury its uppermost (lighter ?) grain.

Subsp. *tectorum* and *lucidus* present a very good, simple and clear example of one of the main processes of adaptive radiation in SW Asia leading to speciation not only in grasses but angiosperms in general. Some of these evolutionary processes have been discussed by Stebbins (1970). Murbeck (1920) also discussed

in length, the importance of synaptospermy in N Africa and Arabian deserts.

5.2 *BROMUS STERILIS* AND THE *B. DIANDRUS-RIGIDUS* COMPLEX

5.2.1. INTRODUCTION

These 3 species are closely related morphologically and constitute a somewhat separate group within *Genea*. There is an almost continuous range of variation in some characters, from *B. rigidus* to *B. diandrus* to *B. sterilis*. Although *B. sterilis* is usually easily separated, the other 2 species are very difficult to separate - at least at the species level. *B. sterilis* is, in habit, the most delicate of the 3 species. It has some similarities to *B. madritensis*, but it is discussed together with *diandrus/rigidus* because it has been regarded as one of the parents of *B. diandrus* ($B. diandrus = B. rigidus \times sterilis$).

B. diandrus and *rigidus* are, in general, robust plants with bigger glumes, lemmas, paleas and awns. In Europe *B. sterilis* is the most common *Genea* species, found almost anywhere, often as a ruderal. It is not common in N Africa nor in SW Asia. It was introduced into N and S America.

In the taxonomic treatment given below, I recognize 2 species: *B. sterilis* and *B. diandrus*. *B. rigidus* is reduced to a variety of the latter. In section 5.2.2.1, I discuss *B. sterilis*; in section 5.2.2.2 I consider *B. diandrus/rigidus*.

B. sterilis has a quite stable morphology throughout its geographical range, is sharply demarcated from most other *Genea* material and poses no complicated taxonomic problems. Contrastingly, botanists have long been aware of the great complexity of *B.*

diandrus and *rigidus*. Their enormous morphological variation has been much discussed and different taxonomic treatments proposed.

In areas where *B. diandrus* and *rigidus* are introduced they have often spread and become naturalized, becoming in some places serious weeds that can affect plantations in general (e.g. S England), sometimes presenting a hazard to grazing animals (e.g. W USA and S Africa). The long awns and the pointed base of lemmas are dangerous if they enter the animals' nostrils, mouth, even flesh or intestines and can reduce the value of the wool. For this reason, *B. rigidus* is sometimes named "Ripgut Grass" in the U.S.A. A better understanding of the diversity of this species complex, as a consequence of the clarification of its taxonomic status is, therefore, of practical importance.

5.2.2 TAXONOMY

5.2.2.1 *B. sterilis*

*B. sterilis** L., Sp.Pl.77 (1753).

Syn.: *Zerna sterilis* Panz. in Denkschr. Akad. Muench. 1813: 297 (1814) - formal combination not made but clearly based on *Bromus sterilis* L.; *Anisantha sterilis* (L.) Nevski in Acta Univ. Asia Med. ser. 8b (Bot.) 17: 20, 22 (1934).

The reason for and the origin of the name "*sterilis*" is not clear. In the pre-Linnaean literature the word "*sterilis*" was not associated with *Bromus* but with *Festuca* and may have been an indication of the apparent worthlessness ("sterile") of a grass when compared with others that could be a food resource as a cereal ("bromos"); (see 3.1.1).

Icon.: Bor, N.L., Fl. Iraq, ed. Townsend *et al.* 9: 158, pl. 54 (1968). Hubbard, C.E., Grasses, 3rd edit., 42 (1985). Penguin Books.

Annual, 4-c.100cm tall, with solitary or loosely tufted, ascending to erect, slender glabrous culms. Leaf sheath softly villous to pilose with retrorse-patent hairs, apically glabrous or occasionally throughout; ligule fringed, acute or round at the base. Leaf blade acuminate, 1.5-23 x 0.1-0.7cm, with short and most often with long hairs also denser on the adaxial surface, very often with longer hairs along the margin continuing along the margin of the sheath near the ligule. Panicle condensed and ascending when young, very soon becoming open, lax, deltoid in outline, up to 17cm long from the lowest to the uppermost node. In very small plants the panicle is reduced to 1 spikelet (var. *oligostachyus* Aschers. & Graebn., *Syn. Mittleleur. Fl.* 2: 592, 1901). Panicle axis usually glabrous, sometimes with short hairs apically. Panicle branches slender, spreading, sometimes with short hairs. Branches longer than spikelets, shorter only when panicle is reduced to 1 or very few (2, 3) spikelets, simple, rarely 1 branch of the lowermost node with 1 ramification, up to 12cm long. Spikelets 1(-2) per branch, cuneate, broadening at maturity when the florets diverge from the axis. Florets 4-12 per spikelet of which 2-4 are sterile. Rachilla segments of very uniform length along the spikelet. Glumes and lemma usually tinged with dark red-purple at maturity, with a narrow hyaline margin, glabrous or with short or long hairs. Lower glume narrowly lanceolate, 1(-3)-veined, 5.5-14.7 x 0.4-1.2mm; upper glume lanceolate, 3(-5)-veined, 7.5-21 x 1.6-3mm. Lemmas of fertile

florets 7-veined, 10.5-30mm long, 2 acute teeth at apex; lemmas of sterile florets smaller. Awn straight, slender, often with a single twist, inserted 1-5mm below the lemma apex; awn length quite uniform in a spikelet, but the awns of sterile florets always shorter and more slender. Awn of second floret 9.5-29mm long. Palea 9.5-17mm long, much shorter than lemma, 2-veined, glabrous on adaxial surface; abaxial surface glabrous or hairy between the veins; veins with long, spreading hairs or short and erect, longer near the apex. Stamens 3; anthers 0.5-2mm long. Caryopsides usually straight, sometimes curved slightly outwards, shorter than palea, 10-15mm long. Callus of rachilla segments differentiated below each fertile floret, obtuse. Scar of rachilla segments round.

Type: While investigating the typification of *B. sterilis*, I came across a major problem in that the proposed lectotype (Smith, 1985) is not *B. sterilis*, that none of the extant Linnaean specimens (at LINN or UPS) and none of the illustrations cited in Linnaeus' *Species Plantarum* protologue are suitable replacements.

Diagnostic features of the lectotype [93.19 LINN] proposed by Smith (1985) compared with my own observations of a wide range of *B. sterilis* specimens:

	[93.19 LINN]	<i>B. sterilis</i>
Panicle branches length (cm)	5 (robust)	Up to 12 (slender)
Lower glume length (mm)	17	5.5-14.7
Upper glume length (mm)	25	7.5-21
Lemma length (mm)	29	10.5-30
Awn	robust	slender
Callus/scar shape	a little pointed/ almost circular	round/circular

These features, together with the overall more robust look of the plant, definitely distinguish it from *B. sterilis*. The description that I give of *B. diandrus* clearly indicates that the specimen is *B. diandrus*. According to the *International Code of Botanical Nomenclature* (1988), Article 69.1, "a name may be ruled as rejected if it has been widely and persistently used for a taxon or taxa not including its type. A name thus rejected, or its basionym if it has one, is placed on a list of nomina rejicienda". For this reason the existing lectotypification would imply the rejection of the name *sterilis*. I do not think that botanists are yet aware of this fact. This is obviously nomenclaturally disruptive because *sterilis* and *diandrus* are two clearly different taxa. The alternative is to conserve the name *B. sterilis* with a new conserved type so as to be able to continue to use this well-established name. Authentic Linnaean material would be ideal and would take precedence for the choice of the type specimen. There is only 1 specimen of *B. sterilis* in Linnaeus' material which is the 93.20 (LINN!). This specimen has the symbol Ø indicating that it was collected in the Middle East; it is also indicated that the specimen was collected by Fredric Hasselquist (1722-52). It is not of major importance that Linnaeus described *B. sterilis* from Europe, but this specimen is better rejected because the Hasselquist specimens were added to Linnaeus' herbarium after *Species Plantarum* was published (1753).

The three references in the protologue are:

- (1) "Bauh. pin. 9", reference to Bauhin, C., *Theatribotanici*: 9 (1623). Bauhin's herbarium is at Uppsala, but I have studied a microfiche and it is very clear that this specimen is *B. arvensis*

L.; (2) "Moris. hist. 3.p.212. f. 8.t. 7.f.11", reference to Morison, R. *Plantarum Historia* ... Part 3: 212; f.8, t.7, f.11 (1680-99). This is the illustration of a grass that could be sterilis. But *B. sterilis* and *diandrus* are too similar to use an illustration that is not totally clear, and could in truth refer to either; (3) "T. Scheuch. gram. 258" is the reference to Scheuchzer, J., *Agrostographia sive Graminum* ...: 258 (1719). The illustration here referred to is of a single spikelet that might be of *B. sterilis*, but obviously is not sufficient to constitute material for a type.

I have discussed these matters in great length with Dr C. Jarvis at the British Museum of Natural History. As a consequence, I have decided to propose [because of the ineligibility of any Linnaean material] a new type specimen for *B. sterilis* selected from any recent herbarium material from Europe. Although I am not doing this formally at this stage I will do so in the future.

Habitats: Europe/Mediterranean - Maquis, in thickets, granite slopes, with *Cercis*, *Pinus brutia*, *Cistus ladanifera*, *Quercus pyrenaica*, *Paliurus*, vineyards; N. Africa - with *Cedrus atlantica*, *Argania*; SW Asia - rocky limestone slopes, scree, in *Quercus* woodland (*Q. persica*, *aegilops*), with *Cercis*; throughout its range - grassy slopes, waste place, roadside, in orchards, hay fields. 20-1500 (-2400)m.

Selection of specimens studied (see p. 48)

EUROPE

Austria. Wien, near Matzleinsdorf, 22 VI 1898, *Krebs* s.n. (E).

Styria: ann. 1842, *Alexander* s.n. (E); Graz, Gösting, 360m, *Fritsch* in *Hayek* 406 (E).

Bulgaria. Sofia, near the airport, 5 VI 1977, *Vihodcevsy* s.n. (SOM). Struma, near Kócerinovo, *Stoeva* 1000 (E). N Bulgaria, Loveč, ann. 1894, *Krumoff* s.n. (SOM).

Czechoslovakia. Brno to Vinohradska, 220m, 7 VI 1962, *Grüll* (E). Kauden, Atschau, *Steltzhamer* 808 (BG).

Denmark. Krstrup, Randers, *Lojtnant* 726 (BG). Zealand, Højby station, *N Jacobsen* 264 (O).

France. Rhone, Arnas, *Gandoger* 389 (O). Ile Vilaine, St Michael, 18 VI 1954, *Stromer* s.n. (O). Pyrenees, *Luchon-Zetterstedt* 389 (O).

Germany. Thuringia, Haustadt, VI 1908, *Reineck* s.n. (O). Bavaria, SE Würzburg, *L. Gross* 473 (BG). Baden, Karlsruhe, *Kneucker* 287 (E).

Greece. E Aegaeon, Psara island, "Ahladhokambos", *Greuter* 10822 (E).

Holland. Den Haag, *Leenhouts* 3380 (O).

Hungary. Budapest, 100m, *Degen* 229 (E).

Ireland. Dublin, Portmarnock, VII 1857, *J. Ball* s.n. (E).

Italy. Pisa, ann. 1846, *Flora Etrusca Exsiccata* s.n. (E). Insula Caprearum, IV 1842, *J. Ball* s.n. (E). Naples, V 1842, *J. Ball* s.n. (E). Sicily, 10mm NE Nicolosi, 1000m, *Davis & Sutton* D. 64447 (E).

- Norway. Rennesoy, Dale, 10 VI 1929, *Holmboe & Lid* s.n. (BG). Rog. Stav. Pedersgaten to Hannesiloen, 18 VII 1983, *Halvorsen* s.n. (BG).
- Portugal. Coimbra, Choupal, V 1880, *Moller* (COI). Alto-Alentejo: Castelo de Vide, 401m, *Beliz* 1530 (ELVE). Torre de Moncorvo, V 1887, *Mariz* s.n. (COI). Madeira, Santo da Serra, *Davis & Macpherson D.* 70993 (E).
- Spain. Sierra de Gredos, El Arenal, 900m, *Deverall & Flannigan* 267 (E). Rio Tiradero, *B.M. Allen* 7529 (E). Malaga, Gobantes to Antequera, *Galiano et al.* 1480.69 (E).
- Sweden. Lund, *Sandin* s.n. (BG). Skane: Helsingborg, 10 VII 1907, *Stensson* s.n. (BG); Paroecia Kävlinge, Kävlinge, *H. Tedin* 258 (O).
- Switzerland. Basel, ann. 1912, *Jermstad* 152 (O). Geneva, ann. 1820, *Blytt* 389 (O).
- Turkey. Istanbul, Yildiz bahçesi, *A. Baytop* 7635 (E).
- United Kingdom. England: Surrey, Tothill near Headley, *Hubbard* 9045 (E); Leatherhead, *H. Burkill* 1531 (E); Sussex, East Grinstead, *Davis* 16930 (E). Scotland: Midlothian, Edinburgh, *Dunnett* 9 (E); Moray, Mains of Craigmell Dallas, *McCallum Webster* 16417 (E); Fife, Burntisland, 22 VII 1848, *Lauder Lindsay* s.n. (E).
- USSR. Crimea: Sokoll, Sudak, *Callier* 232 (O).
- Yugoslavia. Hercegovnia: Trebinje, Golobrd, 12 V 1898, *Baenitz* s.n. (E). Trieste, 3 V 1896, *O. Krebs* s.n. (E). Sarajevo, V 1885, *Beck* s.n. (E).

N AFRICA (+ Canary Islands)

Morocco. Middle Atlas, between Azrou and Timhadite, *Paunero et al.*

1986: 69 (E). High Atlas, Demnate, *Whiting & Richmond* 224 (K).

Immouzer valley, N of Agadir, *Bramwell* 292 (K).

Tunisia. Gafsa, III 1909, *Pitard* s.n. (E).

ASIA

Afghanistan. Kataghan: 25km S Pul i Khumri, 800m, *Rechinger* 33775

(E). Kabul: Kabul, Tang-i Gharu, 1500m, *Hedge & Wendelbo*, W.

2807 (E). Bamian: near Panjao, *Hedge & Wendelbo*, W. 4927 (BG).

Cyprus. Paphos forest, Stavros, *Foggie* 219 (E).

Iran. Lorestan: Ilan, c. 1800m, *Jacobs* 6828 (E); 60km W

Khorramabad, 1160m, *Archibald* 1642 (E). Kerman: Djamal Bariz,

Bam to Djiroft, 2400m, *Rech.* 3878 (E).

Iraq. Baghdad, Jadriyah, *Wheeler Haines* 1615 (E). Kirkuk:

Jarmo, 760m, *Wheeler Haines* 269 (E). Rowanduz: Shaqlawa, 900m,

Wheeler Haines 683 (E).

Israel. Edom, Har Nevo, *Gabrielith* s.n. (HUJ). Mt Carmel, 200m,

Dinsmore 2734 (E). Shomron, Jebel Eteri near Bat Shelomo, 10

IV 1946, *D. Zohary* s.n. (HUJ).

Lebanon. Mt Lebanon, 1600m, 13 V 1877, *J. Ball* (E).

Turkey. Hatay: Kirikhan to Hamam, 100m, *Coode & Jones* 578 (E).

Izmir: Camlibel, Germencik to Selçuk, 200m, *Davis* 41763 (E).

Mardin: Mardin, 1100m, *Davis & Hedge* D. 28365 (E).

USSR. Azerbaidjan: Chatschmas, Chudat to Schollar, *Zakarjan &*

Schevljai 32909 (E). Caucasus: Krasnodar, Gelendzhik, *Litwinow*

4934c (E). Georgia: Tiflis, *Grossheim* 4728 (E).

AMERICA. USA. Washington: Washington, 23 V 1897, *Steele* s.n. (E).

Canada. Vancouver Island, Victoria, 27 V 1893, *Macoun* (E).

AUSTRALIA. W. Australia: Midland Junction, 10 1905, *Staer* (E). S.

Australia: northern Yorke peninsula, *Copely* 768 (E).

Comments on infra-specific variation.

The infra-specific taxa of *B. sterilis* that have been recognized are all at varietal and form rank. Many of them were based on varying pubescence (e.g. f. *glaberrimus* Soó, var. *glabrescens* Zapal/f. *hirsutior* Waisbecker, var. *pilosus* Rohl, var. *pubescens* (Aschs.) Kuntze, var. *velutinus* Volk ex Hegi); others were based on the colour of the lemmas (e.g. var. *purpurens* Schur. var. *viridis* Schur.) and some were recognized for plants with reduced panicles - sometimes to 1 single spikelet (var. *oligostachyus* Aschers. & Graebn.). From my own experience in the field and herbarium, I do not think these infra-specific taxa are worth recognition. Pubescence is very variable in the genus in general and within the same species - as I have referred to in 5.1.2 for *B. tectorum*, that is also the case in this section for the dark red colour of lemmas towards maturity. Finally, phenotypic plasticity plays an important role in the morphological development of these grasses. Small plants and reduced number of spikelets per panicle are frequently a result (as I have observed in the phenotypic plasticity experiment) of poor environmental conditions.

5.2.2.2 *B. diandrus-rigidus* complex

*B. diandrus** Roth, Bot. Abh. 44 (1787).

Annual, 15-120cm tall, with solitary or loosely tufted, ascending to erect, \pm robust culms, glabrous, except for the upper part just below the panicle. Leaf sheath softly villous to pilose with retrorse-patent hairs, wholly glabrous, or only apically or at the base, occasionally glabrous with 2 rows of long hairs along the margins; ligule fringed, acute or round at the base. Leaf blade acuminate, 4.5 x 0.18cm to 22 x 0.85cm with sparse usually long hairs, especially so at margins, somewhat denser on abaxial surface. Panicle condensed and ascending when very young; shape from contracted, stiff erect, narrowly ovate in outline, to lax spreading and broadly ovate; at maturity \pm 1-sided nodding, up to 19cm long from lowest to uppermost node; in very small plants the panicle sometimes reduced to 1-2 spikelets. Panicle axis \pm densely hairy. Panicle branches robust (more rarely slender) straight, erect when young, \pm curved downwards at maturity, shorter than spikelets (sometimes as short as 0.7cm) or longer (up to 14cm), usually single, sometimes the longest lower one with a ramification. Spikelets narrow-ovate, cuneate, tapering when young, usually \pm truncate and broad at maturity but sometimes without change of shape at maturity (in clearly cleistogamous plants), 1.7 - 5.1cm long. Florets (5)6-11, of which (1)2-4 are sterile. Rachilla segments very uniform in length along the spikelet. Glumes and lemma very often dark red-purple at

* *diandrus*: from *diandra*, with 2 stamens; though this is not a regular feature of the species.

maturity with a narrow hyaline margin, with very short or longer hairs at least towards the apex. Lower glume narrowly lanceolate or lanceolate 1(3)-veined, 12 x 1.6mm to 36 x 2.6mm; upper glume more broadly lanceolate, 3(-5)-veined, 18 x 1.4mm to 47 x 3mm. Lemmas or fertile florets 7-veined, 13-53mm long with 2 acute teeth at apex; teeth 0.18-9.5mm long; lemmas of sterile florets smaller. Awn straight, robust, often with a single twist; awn length quite uniform in a spikelet, but awns of sterile florets always shorter and more slender. Awn of second floret 3.5-10.5cm long, often purple sometimes even before maturity and when glumes and lemmas are still green. Palea 10-20.5mm long, much shorter than lemma, glabrous on adaxial surface; abaxial surface glabrous or hairy with short or medium length hairs; short, erect, clearly spaced hairs along the 2 veins, longer near the apex. Stamens 2 or 3; anthers usually 0.45-1.3mm long but up to 5.9mm. Caryopsides straight, c. 0.15mm shorter than palea. Callus of rachilla segments differentiated below each fertile floret, pointed or \pm obtuse. Scar of rachilla segments narrowly elliptic to \pm round.

The description above combines the 2 morphological extremes that so often have been given independent specific status: *B. diandrus* Roth and *B. rigidus* Roth. One of the extremes of the variation is the one represented by plants designated as *B. rigidus*. They are, in general, smaller than *B. diandrus*, with shorter panicles, glumes, lemmas, paleas and awns. They have narrowly contracted panicles, very short and stiff erect panicle branches and the callus/scar of the rachilla segments is

pointed/elliptic. The name *B. diandrus* has been applied to bigger plants with longer, lax panicles, longer panicle branches and longer glumes, lemmas, paleas, awns and anthers. The callus/scar shape of the rachilla segments is most often rounded/circular. However, as discussed later, some of these diagnostic characters are plastic and although some others seem to show some tendency to be associated, any delimitation is very difficult indeed and too many plants remain impossible to place in one of the other extreme (see Appendix 5.2.1). Although there are no differences in geography between these 2 extremes, I have noticed some correlation between ecology [sandy soils, often maritime sand dunes and sandy river banks (*rigidus*) vs. limestone type soils with more humus (*diandrus*)] and some particular morphological features. Plants with the callus/scar pointed/elliptic, short branches, narrow erect panicles more often occur in sandy soils whereas plants with the callus/scar round/circular, long branches, broad, lax panicles, bigger anthers are more often found in heavier, less freely draining soils. This correlation is apparently still weak because in many cases it fails to occur, but it may show an evolutionary tendency in embryo.

All my observations indicate that there are 2 uncertain delimited taxa in this group of plants, but they are not distinct enough to attribute to them a taxonomic rank higher than variety.

Key to the 2 varieties:

1. Panicle contracted, stiffly erect, narrowly ovate; panicle branches mainly shorter than spikelets; anthers up to 0.7mm long; caryopsides usually inrolled, lemma involute with margins touching at maturity; scar of rachilla segments

(Fig.6.2.47)

elliptic; λ base of lemma in side-view straight (Fig.6.2.55).

.....*B. diandrus* Roth var. *rigidus* (Roth) Sales

2. Panicle lax, spreading, broadly-ovate, branches mainly longer than spikelets, sometimes contracted, panicle sometimes with shorter branches especially in specimens growing in conditions of water stress; anthers 0.7-5.9mm long; caryopsides quite often flat, lemma involute with margins not touching at maturity; scar of rachilla segments oval (Fig. 6.2.51); base of lemma in side-view with a constriction at the callus/scar area (Fig. 6.2.56).

.....*B. diandrus* Roth var. *diandrus*

B. diandrus Roth var. *diandrus*

Syn.: *B. gussonii* Parl., Rar. Pl. Sic. 2:8 (1840). *Anisantha gussonii* (Parl.) Nevski in Act. Univ. Asia Med. VIIIb. Bot. 17:20 (1934). *A. diandra* (Roth) Tutin in Clapham *et al.*, Fl. British Isles ed. 2:1149 (1962); Tzvelev in Not.Syst. (Leningrad) 22:4 (1963). *Zerna gussonii* (Parl.) Grossh., Trudy Bot. Inst. Azerbaidzh. Fil. Akad. Nauk. S.S.S.R. 8: 305 (1939).

Icon.: Bor, N.L., Fl. Iraq, ed. Townsend *et al.* 9:143, pl. 48 (1968). Hubbard, C.E., Grasses, 3rd edit., 48 (1985). Penguin Books.

Type: Neotype (selected here): *Gr. Bromoides, locustis maximus, lanuginosum, Italicum*. Hist. Nat.: 261. no. 444 (Scheuchzer Herb., OXF!).

Roth's specimens were destroyed at Berlin (B) in 1943. Although in Roth's protologue of *B. diandrus* there is no

reference to a type specimen nor to locality, there are 2 references that provide some guidance to the choice of a neotype for *B. diandrus*. One is the sentence "*Semina inter passulas majores lecta Majo mense terra comissa plantas nunc (Octobri mense) florentes producerunt*" [seeds collected among big raisins, planted in May and now (October) producing flowers]. This practice of germinating seeds collected from amongst dried raisins was explained in the introduction of Roth's book. He referred there to his interest in the "impurities" (seeds) found among raisins and that he asked merchants for such seeds so that he could grow them in his own garden. Possibly, the *Bromus* "seeds" came from south Germany or Italy. The other relevant reference is to a very good description of the species by Scheuchzer: "Scheuchz., Agrost. pag. m. 261 (descriptio optima)". Scheuchzer in pag. 261 refers to a grass "6. *Gramen Bromoides, locustis maximis, lanuginosum Italicum. Nob.*" that grows in Italy, near Rome and Florence. Among Scheuchzer's specimens at Oxford (OXF) are 2 specimens of *B. diandrus* of which I have seen photographs and photocopies. They are: "*Gr. Bromoides locustis maximis, lanuginosum, Italicum. Hist. Nat. 261. no. 444*" and "*Gramen Bromoides locustis maximis, lanuginosum Italicum Scheuch. Hist. Gram. 261. no. 444*". Both specimens agree well with the original description of *B. diandrus* Roth. I now choose the first one as the type because it is a complete plant, although the other specimen shows better the panicle characters of the species.

Habitats: Open woodland, wet shady ground, shingle banks, edge of stream, maquis, in pasture land, roadside, waste ground, fallow fields, cultivated fields; calcareous, serpentine, clay and sandy soils. From sea level to 1550m (to 2400m in Western America).

Selection of specimens studied (see p. 48)

EUROPE

France. Paris. Côte de Dreux, 9 V 1897, *Jeanpert* s.n. (E). Loire, Nantes, 28 VI 1954, *Stormer* s.n. (O).

Greece. Crete: Ep. Kydonia, Agia, 50m, *Gradstein & Smittenberg* 236 (E). Cos: Cos, s.l. *Davis* 40555 (E).

Italy. Liguria, *Kneucker exsicc.* 653 (E). Trieste, Pola, 21 V 1902, *O. Dahl* (O). Sicily: Palermo, *Todaro* 518 (E). Majorca, Palma, 5 V 1903, *White* (E).

Madeira. Above Poussada dos Vinhaticos, 660m, *Davis* 70741 (E).

Malta, *Somerville* 191 (E).

Norway. Oslo, Gronlien, *Fridtz* 7011 (O). Sogn og Fjordane, Jølster hd., 5 IX 1955, *Befring* (BG).

Portugal. Trás-os-Montes & Alto Douro: Bragança, 720m, *P. Silva et al.* 7592 (LISE). Beira Litoral, ca. 6.5km from Vagos to Ilhavo, *A. Marques* 51 (COI). Estremadura, Loures near Ponte de Frielas 50m, *A. Teles & M. Silva* 1234 (LISE). Algarve, Praia da Rocha, s.l., *Davis* 50970 (E).

Spain. Guipuzcoa, San Sabastian, *Gandoger* 118 (E).

Sweden. Malmo, 18 VI 1920, *Holmberg* (O).

United Kingdom. England: Bournemouth, V 1922, *Sherrin* (BG).

Scotland: Midlothian, Currie to Colinton, VI 1874, *Sadler* (E);

Leith Docks, ann. 1922, *Grierson* (E); Galashiels, Gala water,

O. Stewart 136/74 (E).

Yugoslavia. Croatia: Susak to Martinscicam, 60m, *Degen* ("Gram.

Hung.") 232 (O). Fiume (Rijeka), 20m, *Smoquina* ("Gram. Hung.")

233 (E).

N. AFRICA (+ Canary Islands)

Algeria. Kerrata, 800m, *Reverchon* 274 (E). 03: above Tlemcen, Col

des Zarifète, 1200m, *Davis* 58843 (E).

Canary Islands. Tenerife: 11km E Puerto de la Cruz, 20m, *D. Long*

5567 (E).

Libya. Tripolitania: Marcella, Gargaresh, 15m, *Keith* 872 (K).

Tripoli, nr University of Tripoli, 100m, *Davis* 49453 (E).

Tunisia. NE Cap Bon, La Haouaria to Kelibia, *Davis* 56873 (E).

ASIA (+ Cyprus)

Cyprus. Kyrenia range, Yaila, 800m, *Davis* 2842 (E).

Iraq. Erbil: greater Zab near Eski Kellek, 300m, *Gillett* 8206

(K). Kirkuk: 30km S Durbendikhan, Diyala river, *F. Barkley*

7376 (K).

Israel. Acre Plain, Qiryat Bialik, *Koppel* 11218 (HUJ). Hula

valley, Wadi Dardara, 24 IV 1925, *Smolly* s.n. (HUJ).

Turkey. Adana: Tuzla, s.l., *Coode & Jones* 316 (E). Izmir: Cesme to

Sifne, 30m, *Davis* 41783 (E).

USSR. Azerbaidjan: Apzheronskiy peninsula, E of Baku, 13 V 1952,

Tzvelev s.n. (K).

N. AMERICA U.S.A. Arizona: Chiricahua mts, Barfoot Park, 2440m, *Blumer* 1585 (E). Washington DC, 6 VI 1901, *Steele* s.n. (E). California: Monterey Co., below Big Sur, s.l., *Davis* 66798 (E); Sonoma Co., Santa Rosa, *Heller* 5322 (E).

AUSTRALIA. S Australia: E slopes Mt Lofty range, Monarto South, *Symon* 3120 (K). New South Wales: 18km Goulburn to Yass, Wologorong Creek, *de Nardi* 476 (K). Tasmania: Blackman's Bay near Kingston, *Rodway* 2061 (K).

JAPAN. Honshu: Ishikawa, Taki, Hakui-shi, *Pl. Jap. Exsicc.* 977 (E).

NEW ZEALAND. Clutha railway station, 1 XII 1974, *Hubbard* 9 (K). Kiaora, N Otago, 7 X 1974, *Hubbard* 16 (K).

SOUTH AFRICA. Cape Province: George, XI 1947, *Wilman* s.n. (K); near Muizenberg, 30m, *Crook* 1098 (K).

B. diandrus Roth var *rigidus* (Roth) Sales, stat. nov.

Syn.: *B. rigidus* Roth in Bot. Mag. (Roemer & Usteri) 10 (33): 21-23 (1790). *B. maximus* Desf., Fl. Atl. 1:95 (1798). *Anisantha rigida* (Roth) Hyl., Uppsala Univ. Arsskr. 7:32 (1945). *Anisantha diandra* Roth subsp. *rigida* (Roth) Tzvel., Grasses of the Soviet Union, Part I: 324 (1984).

Icon.: Hitchcock et al. Vascular Plants of the Pacific Northwest.

1. p.512: *B. rigidus* var. *rigidus* (1969). Pignatti, Flora d'Italia, 3, p.526 (1982).

Type: Neotype (here selected): "*Triandria Digynia. Bromus rigidus spiculis multifloris lato-lanceolatis rigidis, floribus diandris, panícula contracta.* Roth, Catal. Bot. 1. p.17. Habitat in Europa australi" (Willdenow Herb., B!).

Roth specimens were destroyed at Berlin (B) in 1943 and there is no reference in the protologue of the description of *B. rigidus* to any specimen. Therefore, a neotype has to be selected. The specimen so chosen is in the herbarium of Willdenow, a contemporary of Roth and on its label is a reference to Roth. The description on the label is the same as in Willdenow, *Sp. Pl.* 5:437 (1801). There are other 3 specimens in Willdenow's herbarium that have the note "*B. rigidus*", but one of them is a different grass and the other 2 have very incomplete labels.

Habitats: Sand dunes, often by the sea, fixed dunes in maquis, riverside, terrace walls (wheat fields in S Africa). From sea level to 950m.

Selection of specimens studied (see p. 48)

EUROPE

Acores. Terceira, Praia da Vitoria, 5m, *Dansereau et al.* 89 (LISE).

France. Vaucluse, V 1844, *J. Ball* s.n. (E).

Greece. Attica, Phaleri, *Orphanides* 1198 (E). Insula Syro, *Orphanides* 1102 (E).

Italy. Sicily: Caltanissetta, 10km W Gela, Manfria, s.l., *Davis* 63222 (E). Sallipoli, ann. 1883, *Groves* s.n. (E).

Portugal. Douro Litoral; Leça da Palmeira, Boa Nova, *Malato-Beliz & Guerra* 13266 (ELVE). Beira Litoral: Ovar, beach of Furadouro, 10m, *Silva et al.* 4566 (LISE). Estremadura: Serra da Arrábida, beach of Creiro, 30m, *Pedro et al.* 177. Arrábida (LISE). Alto Alentejo: Elvas, beside river Guadiana, 158m,

Beliz et al. 351 (LISE). Algarve: Cape St. Vicente, 50m, *Silva et al.* 661 (LISE).

Spain. Sierra de Gredos, N El Arenal, 950m, *Deverall & Flannigan* 0102 (E). Cadiz: Barbate to Cabo Trafalgar, c. 20m, *Davis* 61624 (E).

ASIA

Israel. Coastal Galilee, Akhziv, sea shore, 19 iii 1955, *Feinbrun* s.n. (HUJ). Jaffa, near s.l., *Dinsmore* 1484 (E).

Syria. Caiffa, ann. 1863-64, *Lowne* s.n. (E).

N. AFRICA (+ Canary Islands)

Algeria. Mostaganem, 6 IV 1851, *Balansa* s.n. (E). La Macta, near Mostagenem, 3 V 1936, *Faure* s.n. (E).

Libya. Tripolitania, E Tagiura, *Sandwith* 2062 (K).

Morocco. WS: El Jadida to Azemmour, *Davis* 9407 (E). SW: Essaouira (Mogador), 2m, *Davis* 48353 (E).

Tunisia. N: Ain Sebaa to Jebbara beach. *Davis* 57752 (E). Hammamet, s.l., *Davis* 70171 (E).

Canary Islands. Tenerife: Barranco at Los Arulejos, *Dickson* 105 (E).

AUSTRALIA. New South Wales: Norwood, s.l., VIII 1906, *Black* 3 (K). South Australia: Meningie, 1 VII 1953, *Robertson* 1 (K).

SOUTH AFRICA. S Cape: Riversdale, 60m, *Bohnen* 4531 (K); Cape Town, Malmesbury to Hopefield, *Fourie* 3318 (K).

Comments on synonyms of var. *diandrus* and var. *rigidus*.

B. gussonii Parl. Type : [Sicily] "*In collibus, ad sepes et in sylvaticus frequens occurrit*"

I was kindly sent from the Florence University Herbarium, photographs of 3 Parlatore specimens from Sicily. The general facies of this plant is certainly that of *B. diandrus*, but I have no information about the shape of the callus/scar.

B. hispanicus Rivas Ponce in Lagasalia 3:53 (1973). Type: Spain, arenales del río Tajo en Alconetar (Cáceres), Rivas Goday 3335 (holo-MAF!).

The description of *B. hispanicus* is based on a single specimen. According to its author it differs from *B. rigidus* by its slender awns, oval lodicules, glabrous sheaths and blades; and from *B. diandrus* by its acute callus and longer awns. However, the specimen described by Rivas Ponce comes well within the range of variation I have observed in these 2 taxa. Therefore, I see no reason to consider it as a separate species. Furthermore, this specimen is so much intermediate between *diandrus* and *rigidus* that I cannot assign it to either of its varieties. The long anthers (4mm) of the type specimen are common in *B. diandrus* var. *diandrus* while the degree of pubescence varies more or less continuously within all *Bromus* species.

Characteristic features/measurements of the type specimen:

Longest panicle branch of the first node of the panicle: 5.7cm

Shortest panicle branch of the first node of the panicle: 3.5cm

Callus/scar shape: strongly acute/elliptic

Lower glume length: 19mm

Upper glume length: 39mm

Lemma length: 28mm

Palea length: 14mm

Awn length: 9cm

Caryopsis length: 9mm (but immature)

Anther length: 4mm

B. maximus Desf.*, Fl. Atl. 1:95 (1798). Type: *Gramen avenaceum paniculatum, locustis spadiceo-albidis*. T. Cor. 39 - Vaill. Herb. (holo-P!).

B. maximus is no different from *B. diandrus* var. *rigidus* and should be considered as a synonym of it.

Characteristic features/measurements of the type specimen:

Longest panicle branches of the 1st node of the panicle: 20mm

Shortest panicle branches of the 1st node of the panicle: 3mm

Callus/scar shape: strongly acute/elliptic

Lower glume length: 25-28mm

Upper glume length: 32-35mm

Lemma length: 26-29mm

Palea length: much shorter than lemma

*Desfontaine's herbarium is at Paris (P). The label of the type specimen refers to "ex Cretâ" which is quite surprising because the species was published in Desfontaine's *Flora Atlantica*.

Awn length:	64mm
Caryopsis length:	11-11.5mm
Anther length:	0.7mm

B. rigens L., Mant. Pl. 1:33 (1767).

Often *B. rigens* has been regarded as a synonym of *B. rigidus*. But I have studied the type specimen of *B. rigens* (LINN -93/34) and agree with Bor (1968) that it is a synonym of *B. scoparius* L. (section *Bromus*). The Latin adjectives "*rigidus*" and "*rigens*" both mean stiff or rigid. Certainly because of the similarity between the two words and their meaning, *rigens* was used, wrongly, to designate *rigidus*-like plants. As far as I could trace, this mistake was first made by Dumortier (1823) when he included both *B. rigidus* and *B. rigens* in sect. *Genea*.

B. villosus Forssk., Fl. Aegypt.-Arab. 23 (1775). Lectotype (selected here): Herb.Forskalii no.69 (C!).

B. villosus was first related to *B. rigidus* by Ascherson & Graebner (1901) who considered *B. rigidus* a variety of *B. villosus*. Since then and until very recently, many botanists have wrongly considered *B. villosus* and *B. rigidus* to be synonyms (Täckholm, 1974; Smith, 1981; Meikle, 1985; Feinbrun-Dothan, 1986). I have studied the 4 specimens of *villosus* from Forskål's herbarium (C!) and concluded that all of them are *B. madritensis*. I have chosen as lectotype the most complete specimen and the only one that has a label by Ascherson identifying it as *B. villosus* Forsk. and *B. rigidus* is given as a synonym.

Characteristic features/measurements of the lectotype here selected:

Longest panicle branch of the 1st node of the panicle: 18mm

Lower glume length: 6.5-7mm

Upper glume length: 10mm

Lemma length: 14mm

Palea length: shorter than lemma

Awn length: 20mm

Caryopsis length: 8-10mm

Callus/scar shape: rounded/rounded

5.2.3 MORPHOLOGY

5.2.3.1 Historical

B. sterilis, known for a long time because it is widespread in Europe, has a short taxonomic history. Because of its uniform and clear-cut morphology, it has never been a challenge to botanists. In *Species Plantarum*, Linnaeus described it thus: "*panicula patula, spiculis oblongis distachis, glumis subulato-aristatis*". Over subsequent years botanists have enlarged this description, but there is constant reference in the keys of Floras to its most distinctive characteristics: the broadly lax panicle and the long panicle branches bearing usually one single spikelet.

There is far more to say about *B. diandrus* and *B. rigidus*. Botanists overlooked or neglected Roth's descriptions of *B. diandrus* (1787) and *B. rigidus* (1790) and for a long time these names were not used. The same plants were later described by other botanists with different names; e.g. *B. maximus* Desf. (1798) [= *B. rigidus* Roth] and *B. gussonii* Parl. (1840) [= *B. diandrus* Roth].

These names, *maximus* and *gussonii*, were used at species level and lower ranks, but only rarely in recent times (e.g. *B. gussonei* in Pignatti, 1982). In 1884 Boissier (Fl.Orient.) used the name "*B. rigidus* (syn: *maximus*)" in which he included the var. *gussonei* [sic.]. At the end of the 19th century, Ascherson & Graebner (1901) once again included in one single species - *B. villosus* - all the variants between *B. diandrus* and *B. rigidus* and in their typical polytypic method gave to each of the variants a name and a taxonomic rank. The same procedure was followed much later by Maire & Weiller (1955) and the variations they recognized were those referred to by the French botanists Fouillade (1933) and Cugnac (1934). Although maybe aware that it is often unsatisfactory, contemporary botanists have, with very few exceptions, recognized 2 separate species in this group. Ovadiahu-Yavin (1969) recognized them as 2 subspecies of *B. rigidus*, and Hitchcock *et al.* (1969) as 2 varieties of *B. rigidus*.

The characters most often included in recent keys to separate *B. diandrus* from *B. rigidus* are the panicle (lax and spreading or nodding in *diandrus*; dense and stiffly erect in *rigidus*), the callus (rounded in *diandrus*; pointed in *rigidus*) and the scar (almost circular in *diandrus*; elliptic in *rigidus*). For a more comprehensive list of the characters used in keys see Table 5.2.1. But, from my observations, there is a gradual variation from a dense and stiffly erect panicle (*rigidus*) to a lax and spreading one (*diandrus*). In both species the panicle nods at maturity because of the weight of the caryopsides. In *B. diandrus* the panicle branches are much longer so they droop much more obviously. This is a character often difficult to assess in

TABLE 5.2.1 The most common characters used to separate B. diandrus and B. rigidus in keys.
The variation of each character is analysed and commented on for both taxa.

Character	Character State		Comments
	<u>B. diandrus</u>	<u>B. rigidus</u>	
Panicle	lax; spreading or nodding	dense; stiff erect	There is a gradual variation between the 2 extreme morphologies here referred to. In fact the panicle in both species can nod a little at maturity
Callus	rounded at tip	pointed at tip	These are all intermediates between the 2 extreme morphologies here referred to
Scar	almost circular	elliptic	These are all intermediates between the 2 extreme morphologies here referred to
Panicle branches	equalling or longer than spikelet	mostly shorter than spikelet	These are all intermediates between the 2 extreme morphologies here referred to
Spikelets	spaced and drooping	conspicuously crowded	This is not a good character because it is a consequence of branch length
callus, side view	clearly sticking out of rachilla	not much sticking out of rachilla	This is an interesting character, only used in Floras by Maire (1955), because it relates not only to the callus/scar shape but also to the cleistogamous/chasmogamous condition
Anthers	short or long; included and exerted	short; usually included	This is a good character. Plants that have <u>rigidus</u> features have short, included anthers. Very long anthers (up to 6mm) are not associated only with <u>diandrus</u> features
Culm	almost glabrous	tomentose	In sect. <u>Genea</u> and genus <u>Bromus</u> in general the degree of hairiness varies within a species

herbarium specimens and accurate observations are only possible on living material. The callus/scar shape is very variable and although most plants with *rigidus*-like features have a very pointed callus and a very elliptic scar, *diandrus* can have less typical rounded and circular callus/scar and may even have pointed and elliptic ones (e.g. the type specimen of *B. hispanicus*).

As I have mentioned above, *B. diandrus* has some features intermediate between *B. rigidus* and *B. sterilis*; there has been some controversy about how best to interpret them. Two explanations have been proposed. Cugnac (1931, 1932, 1934) favoured the theory that *diandrus* is a hybrid between *rigidus* and *sterilis*. Fouillade (1933) believed that the polymorphism and intermediate features of *diandrus* are in contrast dependent on the environment, *diandrus* being more *rigidus*-like in difficult, arid conditions and more like *sterilis* in better ones. The question of hybrid origin has been kept open as the only way to conclusively prove it is to produce an artificial hybrid that is *diandrus*-like - which has as not yet been done. Recently, the electrophoretic study of some enzymes and the study of meiosis failed to prove hybrid origin of *B. diandrus*. Common isoforms of malate, alcohol, isocitrate, glutamate and glucose 6-phosphate dehydrogenase and leucine aminopeptidase were rarely found between *B. diandrus* and *B. sterilis* and *B. rigidus* (Esnault-Blanchard, 1981); and all the meiosis studies in *B. diandrus* were very regular (Esnault & Huon, 1985).

As a wider geographic range is studied and more accurate descriptions of the 3 species have been produced, it has become increasingly clear that some of the intermediate characters of *B.*

diandrus described by Cugnac represent in fact only part of the range of variation.

Some intermediate characters, not mentioned by Cugnac, such as the callus and scar shape, certainly need to be better understood, as do their correlation with other characters and their environment.

5.2.3.2 The present analysis

The present analysis was based on extensive herbarium material covering the whole range of native and introduced distribution and also on plant material that was grown in the glass-house in different environmental conditions (plasticity experiments) and on field observations.

The basic characters used to distinguish between *rigidus*, *diandrus* (panicle branch length and callus/scar shape) and *sterilis* (size of spikelet parts) were re-assessed and other characters, such as base of lemma including the callus/scar area, were analysed. Special attention was given to the probable methods of dispersal, and to related structures. Morphological variation was analysed in relation to geography and ecology.

Detailed field observations on dispersal biology of *diandrus* and *rigidus* were carried out in Portugal. Two populations of *rigidus* and occasional plants of *diandrus* were measured for the angle that individual spikelets make with the ground*. In the

* The detailed information that I accumulated is not presented in the thesis, but is available at the R.B.G. Edinburgh; as are the relevant herbarium specimens.

early stages of panicle development of var. *rigidus*, the spikelets are erect making an angle of 0° or nearly so with the vertical. Towards maturity the whole plant bends and the panicle axis droops. Individual spikelets of the lower node of the panicle pass through an angle of 180° , being at the end of the life cycle almost vertically upside down, facing the ground at an angle of more than 45° with it. In cases where the panicle is very condensed and with very few nodes, as I have seen in herbarium specimens of *rigidus*, the panicles seem to remain erect. This could be due to the process of pressing but I believe that it can be genuinely so when the panicle is rather reduced. In *diandrus*, from the very beginning that the panicles are looser than in *rigidus* and in the end the spikelets face the ground vertically.

Pairs of characters were analysed in 75 herbarium specimens to determine any possible correlation. These pairs were: scar length/lemma length; scar length/panicle branches length; scar length/anthers length; anthers length/lemma length. The result of this study (illustrated by scattergrams in Fig. 5.2.1) was that for the pairs of characters analysed, any combination is possible and often character states of typical *diandrus* were combined with typical character states of *rigidus*.

Specimens with very long anthers ("*B. macrantherus*") were investigated. There seems to be a greater frequency of these in the W Iberian Peninsula, in Portugal, but this impression may be due to my own extensive field experience in this area. I have seen other plants with large anthers from N Africa, E Mediterranean, W USA, Australia and New Zealand.

The outcome of a study of this kind, with the whole of the

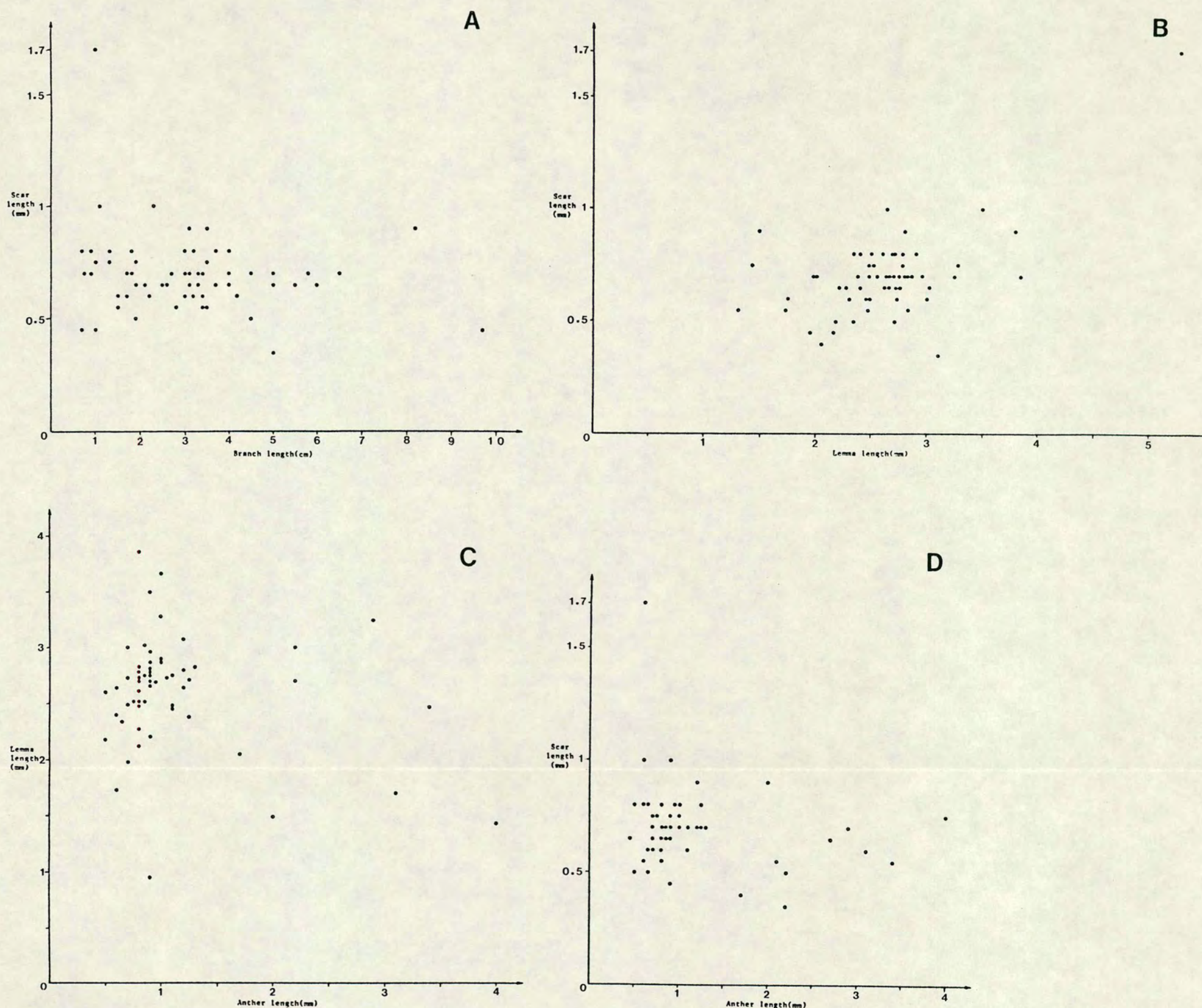


FIG. 5.2.1. Scatter diagrams illustrating the correlation between 4 pairs of characters measured in 75 herbarium specimens of *B. diandrus* var. *diandrus* and var. *rigidus* chosen from a wide range of geographic distribution. The 2 taxa could not be separated by any combination of these characters.

I found that there was a strong correlation between scar length and scar shape: elliptic scars tend to be longer than rounded ones. For this reason, scar length was used because it is a more objective feature.

- A. There is a continuous range of variation of these 2 characters, probably connected with the high phenotypic plasticity of the panicle branches. However, in some cases, long scar is associated with very short panicle branches in typical var. *rigidus*, and short scar associated with very long branches in var. *diandrus*.
- B. There is a continuous range of variation of these 2 characters. Note that very long scar (1.7) can be associated with very long lemma (53).
- C. Longer anthers are rarer and are associated with a wide lemma size.
- D. Longer anthers are more associated with var. *diandrus*-scar shape. Small anthers are combined with a wide range of scar length.

geographical range of variation taken into account, was the conclusion that the differences between var. *diandrus* and var. *rigidus* are often so subtle that the identification of many specimens cannot go any further than a mere *B. diandrus* s.l.

5.2.3.3 Notes on particular features

Branch length of panicle

The length of panicle branches is quite plastic in *B. sterilis* and *B. diandrus* var. *diandrus*. Although typically the branches are longer than the spikelets, in poor water conditions the length and number of branches, and as a consequence the number of spikelets, is much reduced. As I have observed in the phenotypic plasticity experiment, *B. sterilis* growing in dry conditions has a single spikelet. However, the variation on the panicle branches in *B. diandrus* s.l. seems to be in some cases more than a plastic character. On one hand, specimens of var. *rigidus* that grew in non-restricted water conditions had a little longer branches than their water-stress counterparts, but they still had quite short branches and contracted panicles. On the other, in the survey of the herbarium specimens, I found that long panicle branches are strongly associated with features of var. *diandrus* (more rounded callus/scar, longer anthers and base of lemma with a constriction at the callus/scar area - see following subsection) although there are a few exceptions; but short panicle branches linked both with the typical var. *rigidus* morphology and to a greater extent with var. *diandrus*. Therefore, the short branches cannot be a mere reduction induced by the environment. It is often difficult to judge when this is the case and therefore the relevance of this

character on its own is very limited.

Callus and scar shape

Although used so often as a valuable taxonomic character there is a great variability of callus and scar shape and there is no clear delimitation between the so-called elliptic morphology usually associated with *rigidus* (Fig. 6.2.47) and the ovate one associated with *diandrus* (Fig. 6.2.51). I found also that there is no clear delimitation between the ovate shape in *diandrus* and the round shape of the callus/scar in *sterilis* (Fig. 6.2.52). The intermediate morphologies between *rigidus*, *diandrus* and *sterilis* are strikingly illustrated in Figures 6.2.47-54. In spite of this continuous variation, it is still possible to a degree, to relate the elliptic/pointed, the ovate/round and the circular/round callus/scar to *B. rigidus*, *diandrus* and *sterilis* respectively. It is clear that the character of callus and scar shape, as well as branch length, cannot be used alone to distinguish the 3 taxa. However, *B. sterilis* can easily be separated from the other 2 because of the smaller size of the reproductive parts.

I consider that the callus/scar area must play a more important biological role than has been recognized thus far. It is highly likely that a pointed callus serves a significant function in the burial of the grain. When the grains are heavy and the soil is soft, pointed lemmas associated with rough awns, can be very effective for propagule, anchorage and/or burial. Typical var. *rigidus* combines all these morphological features, and it is surely significant that it is common in sandy soils. I did some field work in the coast line of central Portugal which contains

extensive sand-dune systems. Here, only var. *rigidus* grows. At the end of the life cycle (July) the whole plant drops until the panicle almost touches the ground. Only then do the spikelets fully disarticulate. Many of the grains are very effectively and swiftly buried in earth just below the panicle. The functional significance of this morphology can, therefore, scarcely be discounted.

The late dispersal of some of the florets in var. *rigidus* is not due to a late development of the callus/scar, but to its shape and to the spikelet structure. The forms of var. *rigidus* with very small panicles do not nod and the panicles remain erect during the whole of the life cycle. In these forms a few top florets detach earlier but the lower ones remain together because they are part of a quite rigid structure. On one hand, the much longer scar offers a longer surface of contact between lemma and rachilla (Figs 6.2.48-51); on the other, the florets are so imbricated with each other that the time for dispersal takes longer. The reason why the florets imbricate so well is related, once again, to the morphology of the callus/scar area. In *Genea* (indeed, in many other *Bromus* species) the florets \pm diverge from the rachilla axis towards maturity, but this does not happen in var. *rigidus*. For the florets to diverge it is necessary to have a point of articulation at the base of the lemma, as shown as a constriction in *B. sterilis* in Figures 6.2.56 and 5.2.2. Towards maturity the angle between the scar (rachilla axis) and the lemma at this articulation region widens (Figs 5.2.2.b) so that the whole lemma is separated from the rachilla axis. Apart from this, in some cases the curving of the rachilla segments themselves provides an

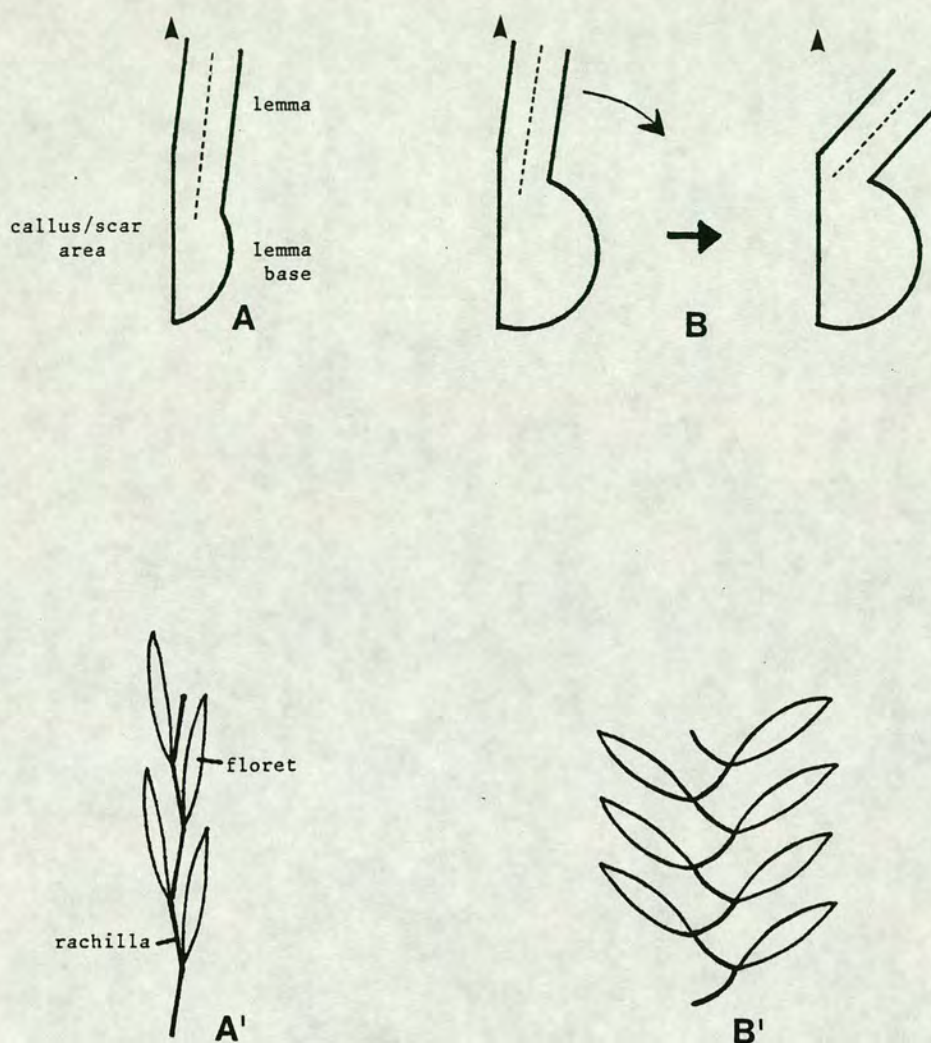


FIG.5.2.2. Articulation/non-articulation of florets in a spikelet in B. diandrus var. diandrus and var. rigidus.

- A. B. diandrus var. rigidus: relative position of floret in relation to the spikelet axis (▲) at a young stage and at maturity; note the non-articulation of lemma with its base.
- B. B. diandrus var. diandrus: relative position of floret in relation to the spikelet axis (▲) at a young stage and at maturity; the articulation of the lemma with its base moves the floret upwards.
- A'. B. diandrus var. rigidus: portion of spikelet; there is no change of the shape of the rachilla segments towards maturity; this, combined with the non-articulation of the lemma with its base (A), results in very condensed spikelets at the end of the life cycle.
- B'. B. diandrus var. diandrus: portion of spikelet; the rachilla segments curve towards maturity (here exaggerated for clarity); this, combined with the articulation of the lemma with its base (B), results in wider open spikelets. The same sequence of events happens in other Genea species, especially B. sterilis, B. madritensis and B. fasciculatus.

extra widening for the whole structure (Fig. 5.2.2.b'). In contrast, a callus/scar elliptic/pointed as in var. *rigidus* is always associated with lemmas without the previously mentioned articulation area, as shown in Figure 6.2.55. For this reason, the florets remain condensed (Fig. 5.2.2.a), which is further emphasized and effected by the rachilla segments remaining straight (Fig. 5.2.2.a'). All these mechanisms permit the quite narrow lemmas and grains of var. *rigidus* to remain imbricate, even when sometimes the single florets are already physically detached from each other at the callus/scar area.

The late dispersal in sect. *Bromus* due to the same kind of imbrication is a consequence of some different factors. Lemmas in sect. *Bromus* are ovate, quite broad and often spreading and surrounding the lemma immediately above it, holding it in position, and in a few cases abscission does not naturally occur (e.g. *B. pseudosecalimus*).

The different shapes of the scar correspond to different degrees of development of the articulation area at the base of the lemma. Var. *diandrus*, with an ovate callus intermediate between the elliptic one of var. *rigidus* and the circular one of *sterilis*, has an articulation area less developed and constricted as in *sterilis*. Further, the intermediate morphologies of callus/scar between *diandrus* and *rigidus* also present an intermediate degree of constriction at the lemma base. In *B. diandrus* s.l. there are therefore 2 well-defined extreme morphologies summarized below:

- var. *rigidus*: a condensed panicle with erect, short panicle branches; imbricate, less exposed florets and rachilla segments; stamens inserted with very small anthers;

- var. *diandrus*: a lax panicle with loose, long panicle branches; spreading exposed florets and rachilla segments at flowering stages; stamens inserted with longer anthers or obviously exerted with very long anthers.

In var. *rigidus* all the reproductive structures seem to be protected from the pollinator agent in the grasses, the wind; while in var. *diandrus* they seem to be singularly exposed thus favouring ^{occasional} cross-pollination. But in my opinion the combination of all these factors and morphological differences are part of an even more general mechanism of adaptive radiation that I will discuss in Chapter 9.

Once again I stress the existence of numerous intermediates regarding all the characters and an incomplete, unclear ecological or geographic separation, thus accounting for the varietal rank I have given to both. Nevertheless, I would say that there is in var. *rigidus* a different biological "approach" to the environment. I consider that the differences between both varieties are significant, but not yet distinct enough for a higher taxonomic rank. In the fulness of time and with unchanged selection pressures, these minor taxa may eventually further diverge, eventually meriting higher status.

The lack of evidence, so far, that *B. diandrus* var. *diandrus* has an hybrid origin strengthens my belief that the real morphologically intermediate position of this taxon is due to: 1) closeness to *B. sterilis*; 2) recent evolution and incomplete separation of *B. diandrus* var. *rigidus* from var. *diandrus*.

5.3 *BROMUS MADRITENSIS*, *B. HAUSSKNECHTII*, *B. RUBENS* AND *B. FASCICULATUS*

5.3.1 INTRODUCTION

These taxa are separated from the other *Genea* species by the combination of the characters of small lemmas and erect, contracted panicles. *B. madritensis* occupies a rather intermediate position between this group and that of *B. sterilis* because it often has looser and more open panicles. The number of species that should be recognized in this group is uncertain; many, for example, consider *B. haussknechtii* as merely a depauperate form of *B. madritensis*.

All the species of this group are mainly Mediterranean, with some extensions into SW Asia. The most lax-panicled forms of *B. madritensis* colonize some areas in central and atlantic Europe, but only *B. rubens* is naturalized in large areas of the New World. In the USA it is, like *B. tectorum* and *B. rigidus*, an undesirable weed. At the other extreme are *B. fasciculatus* and *B. haussknechtii* with restricted distributions being mainly confined to the E Mediterranean and more western parts of SW Asia. In particular, *B. fasciculatus* thrives in very dry places, even in deserts, both in N Africa and SW Asia. It is a particularly frequent species in Israel and adjacent areas.

As in the other groups of *Genea* species, this one has great morphological variation and it is difficult to define precisely the boundaries of the constituent taxa. It is worth mentioning that herbarium collection in this group in general, and *B. fasciculatus* in particular, are poor. Many specimens have no field observations on their labels and rarely there is not even a

precise locality (e.g. "*Arabia Petraea*"). Although in some field notes, as well as in some Floras, there is mention of well-established and numerous local populations, the number of ideal herbarium specimens is relatively small.

I have concentrated my work in this group on *B. fasciculatus* because I felt I could contribute towards the clarification of some of its nomenclatural problems and better define its geographical distribution and ecology. Although my observations on the other taxa of this group enabled me to develop a critical overview of them, I was unable, because of the time factor, to investigate them in the detail required. I will not, therefore, propose definite taxonomic conclusions, but merely point out a few new aspects and suggestions for the way ahead in understanding the puzzle posed by the great variation of *B. madritensis* and its close allies.

5.3.2 *B. MADRITENSIS*, *B. HAUSSKNECHTII* AND *B. RUBENS*

B. madritensis is a highly polymorphic species, sometimes with longer panicle branches and looser panicles, but quite often with more *rubens*-like condensed panicles. The great number of imprecise subspecific taxa that have been or are recognized within *B. madritensis* and *B. rubens* mirrors the difficulties that botanists have had in understanding both their morphological variability and their similarities.

B. madritensis and *B. rubens* have traditionally been separated as independent species on the basis of panicle shape, branch length and division, spikelet length, lemma length and width. But the character state of these characters often overlap and some

are plastic (Esnault, 1984; and personal observations). They are, therefore, not precise enough to clearly separate the taxa.

An intensive overall taxonomic revision is much needed to assess the value of: [1] the traditional characters and recent assessment of them (*B. madritensis*, Esnault, 1984); [2] recently proposed characters, such as panicle structure (Rivas Ponce, 1988); [3] weighting of certain morphological aspects (such as the structure of sterile florets, Scholz, 1981) that are related to the dispersal biology.

At present, I incline to think that all the material is of one species. If *B. madritensis* and *B. rubens* have to be combined, it appears that the epithet to be adopted is *B. madritensis*. It should be noted that both species were described by Linnaeus in *Cent.Pl.* (1755); and were first combined as *B. madritensis* subsp. *rubens* by Husnot in 1899.

At the boundary between *B. madritensis* and *B. rubens* there are taxa that have been named *B. madritensis* subsp. *Kunkelii* H. Scholz (*Willdenowia* 11: 249-258, 1981) and *B. haussknechtii* Boiss. (*Fl. Orient.* 5: 648, 1884). I have studied the type specimens of these 4 taxa and my observations are summarized in Table 5.3.1. *B. flabellatus* Boiss. is another taxon within this group; I have not studied its type specimen ("prope Hierosolymam", Jerusalem), but from its description it also seems to be intermediate between *B. madritensis* and *rubens*.

I believe that an extensive investigation of the variation in this group will drastically reduce the number of species (and infraspecific taxa) that merit formal recognition.

TABLE 5.3.1 Diagnostic features of the type specimens of B. madritensis, B. madritensis subsp. kunkelii, B. haussknechtii and B. rubens, based on my own observations.

Characters	<u>B. madritensis</u>	<u>B. madritensis</u> subsp. <u>kunkelii</u>	<u>B. haussknechtii</u>	<u>B. rubens</u>
Culm pubescence	glabrous	hairy below panicle	-	hairy below panicle
Panicle length including awns (cm)	13	6.5 - 8.5	7.5	7.5
First panicle internode (cm)	1.7	-	1.4	1.3
Panicle branches (longest of lower node)	Posture Length Longer Shorter Division Pubescence	loosely erect 19 - 1	erect 8 2 2 hairy	erect 0.9 - 2(1) many short hairs
Spikelet size (mm)	5 - 5.4 (in- cluding awns)	2.3/2.9	-	3.7-3.9 (in- cluding awns)
No. florest	Fertile Sterile	- -	5 6	- -
Lower glume (mm)	9	9	5.3	8
Upper glume (mm)	14	11.2	8.5	11
Lemma (mm)	17	18	10.3	15
Awn (mm)	2 - 2.1	13.5	10.4	19-20
Palea (mm)		14	8.2	
Anthers (mm)		0.7	0.6	
Caryopsides (mm)	-	-	8	10

5.3.3 *B. FASCICULATUS*

5.3.3.1 Taxonomy

*B. fasciculatus** C. Presl, Cyp. Gram. Sic. 38 (1820).

Syn: *B. madritensis* L. var. *delilei* Boiss., Fl. Orient. 5: 649

(1884); *B. rubens* L. subsp. *fasciculatus* (C. Presl) Trabut in Batt. & Trab., Fl. Algér. Mon. 226 (1895); *B. fasciculatus* C. Presl var. *alexandrinus* Thell. in Feddes Rept. 5: 161 (1908);

Anisantha fasciculata (C. Presl) Nevski in Acta Univ. Asia Med. Ser. 8b (Bot.) 17: 21 (1934);

Bromus fasciculatus C. Presl var. *fallax* Maire in Bull. Soc. Hist. Nat. Afr. Nord. 33: 97 (1942);

B. fasciculatus C. Presl subsp. *delilei* (Boiss.) H. Scholz in Willdenowia 6: 291 (1971).

Icon: Bor, N.L., Fl. Iraq, ed. Townsend *et al.* 9: 145, pl. 49 (1968). Täckholm, V., Students' Fl. Egypt, ed. 2, pl. 251A (1974). Plitman, U. *et al.*, Pictorial Fl. Israel, p. 345 (1983).

Annual, 7-30cm tall, with tufted, sometimes solitary, slender culms, usually geniculate at base, glabrous, puberulous below the panicle or with very short hairs. Basal leaf sheath with short, retrorse or retrorse-patent hairs or longer woolly hairs, occasionally glabrous throughout; ligule fringed, acute or round at base. Leaf blade acuminate, 2-8 x 1-1.8cm with short or longer

* Presl did not indicate why he named his species "*fasciculatus*", but the panicle is a fascicle, or bundle of spikelets, and this must be the reason why he used it.

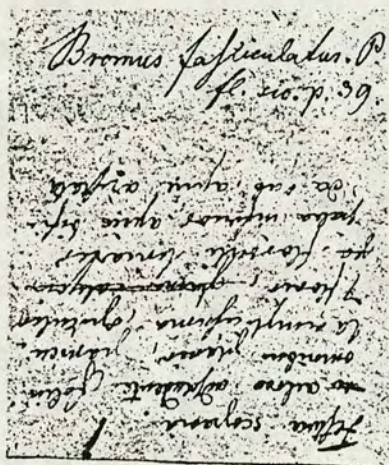
hairs \pm equally dense on both surfaces. Panicle flabellate, at least at maturity, markedly cuneate at the base, stiffly erect, usually condensed (in very dwarf plants reduced to (1)-2 spikelets), 3-7.5cm long including the awns, up to 3.5cm from the lower to the top node. Panicle branches simple or with ramifications, very short. Panicle axis and branches glabrous or hispidulous. Spikelets lanceolate at earlier stages when glumes and lemmas are strongly imbricate, soon broadening becoming flabellate, 20-30mm long excluding awns, up to 8mm wide, cuneate at base, compressed, with florets well-separated at maturity. Florets (6)-10-15 per spikelet with 2-3 uppermost ones sterile. Glumes and lemmas narrowly lanceolate, dark purple at maturity with a hyaline margin, variously hairy sometimes ciliate at margins, more rarely glabrous, lower glume 1-veined, 6.7-8 x 0.6-0.9mm, upper glume 3-veined, 10.8-12 x 1.4-1.6mm. Lemmas 7-veined, 11-16 x 1.3-1.8mm, 2-toothed, margins usually overlapping at maturity. Awn straight only when very young, soon curving both outwards and upwards, twisted, inserted 1.5-3.5mm below lemma apex, as long as or a little longer than lemma; awn of second floret 14-18mm long. Palea little shorter than lemma 9.5-13mm long, glabrous on adaxial surface; abaxial surface glabrous or hairy. Stamens 3; anthers 0.3-0.5mm long. Caryopsides needle-like, curved outwards, \pm twisted, often inrolled, 7-12.7 x 0.25-0.5mm. The combined twist of caryopsides and awns often gives an overall twist to the whole spikelet. Callus of rachilla segments round or oval.

B. fasciculatus differs from *B. rubens* by the generally flabellate panicle and flabellate mature spikelets, narrow glumes

and lemma, recurved awns, outcurved and often twisted grain and straight rachilla segments of the top sterile florets.

Type: Sicily; "in arvis arenosis, Panormi in planitie della Cunzulazione (PR!). In the protologue Presl described *B. fasciculatus* as: "panic. simplicissima, locustis 7-floris, flosculorum linearium palea inferior apice bifida, arista paleam aequante, fol. planis culmoque adscendente glabris".

Presl's herbarium is in Prague (PRC) whence I was sent, on request for the type, a herbarium specimen collected in Sicily in 1817 with a label presumably handwritten by Presl himself:



This specimen is a mixed gathering of several specimens of *B. fasciculatus* and another grass, probably *Vulpia*. Although the name *Festuca scoparia* occurs on the label, the description on the label is remarkably similar to Presl's later protologue of *B. fasciculatus* (1820). I doubt if this specimen has previously been recognized as the holotype of *B. fasciculatus*. However, I consider

that I have assembled enough information to cite it as such.

Diagnostic features of the type specimen based on my own observations:

Habit: tufted and solitary plants, geniculate at base.

Height: 6-16cm.

Leaf sheath hairiness: short, retrorse and woolly hairs.

Panicle shape: flabellate, strongly cuneate at base, stiffly erect, dense; some panicles with only 2 spikelets.

Panicle length: 3-5cm; axis length up to 2cm from the lowest to the top node.

Spikelet shape when young: lanceolate, glumes and lemmas imbricated.

Spikelet shape when mature: flabellate, cuneate at base, compressed, florets well-separated at maturity.

Lower glume size: 7-7.5 x 0.8mm

Upper glume size; 8.6-10.2 x 1-1.4mm

Lemma size: 13.5-14.5 x 1.2mm

Lemma hairiness: glabrous or with very short hairs.

Awn posture: curved outwards and upwards, twisted.

Awn insertion: 3-3.5mm below lemma apex.

Anther length: 0.4mm.

Caryopsides shape: needle-like, curved outwards and twisted, inrolled.

Caryopsides size: 10 x 0.4mm.

Callus shape: ovate.

Habitats: Europe-Mediterranean area: dry places in general; maritime sands, calcareous soil and grassy areas, sometimes along roads. N Africa and SW Asia: along the coast, in wadis, dry steppe and desert; in maritime and desert sands, rocky places, sandy loam, limestone, calcareous, gravelly clay soil, granite, basalt and andesite (in Saudi Arabia); in limestone macchie with *Juniperus phoenicea* and *Pistacia lentiscus* in Libya. Sometimes in classical ruins. Very common in some localities in Cyprus, Israel, Saudi Arabia (Taij Mountains) and Iraq. From 5-1220M, up to 2133M in Saudi Arabia and to -380M in the Dead Sea area.

Selection of specimens studied (see p 48)

EUROPE

Greece. Crete: Akrotiri, Korakies hills, 200M, *Rechinger* 13293 (BM). Kos: Kos town, *Brenan* 11175 (K). Rhodes: *Rechinger* 8373 (K).

Italy. Euraia: Isle of Pianosa, 5-30M, *Sommier* 1220 (K). Sicily: Syracuse, *Bucknall & White* 506 (E).

Malta. *Sine loc.*, *Wright* 681 (K).

Sardinia. Antioco, IV 1828-9, *Müller* s.n. (K). Torre delle Stelle, 30 VI 1981, *Hygür* s.n. (O).

N AFRICA

Algeria. Oran: Djebel-Santo, *Balansa* 298 (E).

Egypt. Gebel Atagga, 600-800M, *Davis* 6592 B (E). Wadi el Arish, *Simpson* 2565 (K). Mariut: Abu Sir, *Davis* 6498 B (K).

Libya. Benghazi prov.: 30km S Agedabia, *Simpson* 39079 (K). 5km W Baiadas, 300-350M, *Davis* 49954 (K).

ASIA (+ CYPRUS)

Cyprus. Lacovounera forest, 183M, *Chapman* 358 (K).

Iraq. DWD: Jabal Ana, 100-150M, *Khayat & Hamal* 51745 (K). DSD:

12km ESE of Salman, 240M, *Guest et al.* 18848 (K). FUJ. Jebel

Makkul near Ajn dibbs, 250M *Gillett & Rawi* 7208 (K).

Israel. 54km N Eilat: Arava Valley, 13 III 1951, *Orshan & Zohary*

s.n. (HUJ). Near Ballut: 35°E 32°N, 26 IV 1919, *Ogilvie* s.n.

(K).

Jordan. Transjordan: Wadi Ram, 914M, *Davis* 9007 (K). Azraq Druze,

Townsend 65/318 (K).

Lebanon. Beirut, *Herb. Post.* 163 (K).

Oman. 45km SW Muscat: Jebel Aswad, 1371M, *Munton* 16 (K).

Saudi Arabia. Jiddah-Taij road, 1066M, *Collenette* 3983 (K). 85km

SW Tabut: Jabal Dabbagh, 1371M, *Collenette* 4396 (K). 80km SW

Madinah: Jabal Warjan, 2133M, *Collenette* 5225 (K). Taif

Highlands, 21°10'N 40°20'E, 2133M, *Fitzgerald* 17060/4 (K).

Syria. Damascus, *Pastuchov* 730 (LE). Palmyra, 435M, *Samuelsson*

3514 (K).

Turkey. C3: Antalya Konya Alti, 10M, *Tengwall* 436 (K).

5.3.3.2 Morphology

5.3.3.2.1 Historical

The name *B. fasciculatus* was published in 1820 by Presl based on a specimen from Sicily. It is of historical interest that it seems there was an earlier recognition of this taxon, but a description of it was not published. The herbarium at Edinburgh (E) holds several presumed Delile specimens collected by himself in 1801 (when he was with Napoleon's army in Egypt) or else

gathered by his co-collectors. These specimens can be easily recognized because of the characteristic handwriting on the labels. One of these specimens at Edinburgh is clearly *B. fasciculatus*, but its label is:

Bromus hexastachyos Del. Catal
Nouvelle Espèce

Egypte

"*Bromus hexastachyos* Del. Catal. [possibly a manuscript catalogue housed at Paris (P) or Montpellier (MPU), - pers. inf. I.C. Hedge] n[ou]velle Éspèce, Egypte". Although Delile published similar names, e.g. *B. distachyos*, the name *B. hexastachyos* was never validly published, nor does it occur as a *nomen* in Delile's *Flora of Egypt*, where the only relevant *Bromus* listed and illustrated is *B. rubens* (*Fl. Aegypt. Illustr.* pl. 11, fig. 2, 1813). It is most interesting that this illustration is in fact a good one of ... *B. fasciculatus*! Later on Boissier (*Fl. Orient.* 5: 650.1884), recognizing the identity of the 2 taxa, cites *B. rubens* sensu Delile as a synonym of *fasciculatus*. It seems that initially Delile thought that the dwarf grass, with geniculate and tufted culms, flabellate panicles and curved awns he found in Egypt was a new species but later, recognizing some similarities between this

plant and *B. rubens*, gave up his first idea and determined "*B. hexastachyos*" as *B. rubens*.

Since the time that it was validly published in 1820, *B. fasciculatus* has generally been recognized as a separate species. However, because of its cuneate, condensed small panicles it has also been placed with *B. rubens* (*B. rubens* L. subsp. *fasciculatus* (Presl) Trabut) and, because of its dwarf appearance, with depauperate forms of *B. madritensis/haussknechtii* (*B. madritensis* L. var. *delilei* Boiss.)

The taxonomic situation of *B. madritensis* var. *delilei* is a rather complicated one. Its type locality is "Egypt/circa Alexandrian (Delile)" and Boissier cites as second localities - "in deserto Aegyptiaco-Arabico variis locis (Schweinfurth 28! 130! 253! et 456!) plus a reference to "*B. rubens* Desf., Ill. p.164, t.11, fig.2". Surely there is a mistake in this last reference because there is no illustration of *B. rubens* in any of Desfontaine's publications. In fact, Boissier was certainly referring to Delile's *Fl. Aegypt.Illustr.* pl.11, fig.2, 1813, which brings us again to "*B. hexastachyos*". In Boissier's Herbarium (G-BOISS) there are only the Schweinfurth specimens, which I have studied. The Delile specimen is not in the Delile herbarium at Paris (P) but may be at Montpellier (MPU). I have not seen this Delile collection, but would not be surprised if the probable Delile specimen at Edinburgh (E), "*B. hexastachyos*", is in fact an isotype of *B. madritensis* var. *delilei*. However, Scholz (1971) designated as lectotype for this taxon, unwisely in my opinion, one of the Schweinfurth specimens cited in second place by Boissier (*Schweinf.* 456). In fact, apart from being cited in

second place, Schweinfurth's specimens cited by Boissier are a mixed gathering: one is *B. fasciculatus* (Schweinf. 456, the lectotype chosen by Scholz); another, which Boissier described on the previous page (*Fl. Orient.* 5: 648, 1884) as a new species from Baghdad, related to *B. madritensis*, is *B. haussknechtii* (Schweinf. 28). The other 2 specimens are mixtures of both *fasciculatus* and *haussknechtii* (Schweinf. 130 and 253). The description of *B. madritensis* var. *delilei* is not precise and fits both *fasciculatus* and *haussknechtii*. In the absence of Delile's Egypt-Alexandria specimen that might clarify Boissier's concept of var. *delilei*, it is unwise to lectotypify it with a *fasciculatus* specimen. In fact, it is better not to use the name at all because its application is very confusing. If the plants which are, in reality, *haussknechtii* were placed by mistake in var. *delilei*, so also may the *fasciculatus* ones. This is because Boissier lists this last species separately in the same work (*Fl. Orient.* 5: 650, 1884). I have studied the type of *B. haussknechtii* at Geneva (G). It is a taller, more robust plant than the specimens included in var. *delilei* and this may be the reason why they were placed separately.

Although I suspect that nobody has studied the Montpellier type specimen of var. *delilei*, this taxon has been included in *B. madritensis* at subspecific level (Maire, 1955; Ovadiahu-Yavin, 1969), but more generally considered as a synonym of *B. fasciculatus* (e.g. Bor, 1968; Scholz, 1987).

The other taxon often recognized in *B. fasciculatus* is *B. fasciculatus* var. *alexandrinus* Thell. (1908), based on a well-developed indumentum ["... ramis inflorescentiae ... pubescenti-

velutinis, spiculis longe ciliato-villosis"] (e.g. Bor, 1968; Ovadiahu-Yavin, 1969; Täckholm, 1974; Feinbrun, 1986).

More recently, Scholz (1971) recognized 2 subspecies in *B. fasciculatus*, the type subspecies and subsp. *delilei* (Boiss.) H. Scholz. In an expanded work on both taxa, Scholz (1987) described them in the following way:

subsp. *fasciculatus* - "Lemma callus ... basal boundary line parabolic, ... lower leaf sheath with dense villose hairs restricted to the mediterranean area but including Palestine coastal areas;

subsp. *delilei* - "Lemma callus ... basal boundary line semi-orbicular, ... lower leaf sheaths with dense to sparse short hairs" in the West Irano-Turanian area.

Most of the infraspecific taxa in *B. fasciculatus* were based on differences of pubescence. Only Scholz (1987) drew attention to a new character in this group: the shape of the callus/scar, already used for *B. diandrus/rigidus*, and pointed out a connection of this character with distribution.

5.3.3.2.2 The present analysis

The present analysis is based on the macro-morphological observation of 100 specimens covering the whole range of distribution.

B. fasciculatus has a quite uniform morphology. Variation concerns mainly the number and length of culms per tuft and number of spikelets per panicle. These variations are surely related to environmental conditions. There is also great variation in the degree of pubescence and some variation in the shape of the

callus/scar on the rachilla segments.

5.3.3.2.3 Notes on particular features

PUBESCENCE

The infraspecific classification of *B. fasciculatus* has been almost entirely based on the different degrees of pubescence on leaf sheaths, culms, panicle branches, glumes and lemmas. During my studies, I found great variation both in the type and the degree of pubescence on the whole plant. I found it quite impossible to establish a clear distinction between the different types described. In my experience, pubescence is not a reliable character in *Genea* or indeed in the whole genus. Plants that I grew in the plasticity experiments showed that *B. rubens* has a random and small variation of the indumentum under different treatments, while *B. madritensis* reveals some degree of plasticity in this character. In *B. madritensis*, plants that grow in poorer conditions tend to have fewer and shorter hairs.

Pubescence on glumes and lemmas has most often been used taxonomically in *B. fasciculatus* (Maire, 1955; Bor, 1968; Ovadiahu-Yavin, 1969; Feinbrun-Dothan, 1986): glabrous versus pubescent; pubescent with or without cilia at margins. But I have found other combinations:

- glabrous, but with cilia at margins;
- different degrees of density of hair coverage including cilia;
- different degrees of the length of hairs including cilia.

As noted above, Scholz (1987) using the characters of the pubescence of the lower leaf sheaths together with the shape of the callus/scar on rachilla segments and geography divided *B. fasciculatus* into 2 subspecies: subsp. *fasciculatus* with leaf sheaths densely villous and callus/scar pointed/ovate, from the Mediterranean area; and subsp. *delilei* with dense to sparse, short hairs and callus/scar round, from the W Irano-Turanian region. However, I found different degrees of pubescence in both geographical areas and even in different plants of the type specimen of *B. fasciculatus*. The variation is continuous in the total range, from totally glabrous to an indumentum of numerous long hairs giving a woolly cover. I, therefore, consider the pubescence of leaf sheaths of no taxonomic importance.

CALLUS/SCAR SHAPE

My observations have confirmed the existence of 2 different forms of the callus/scar and a geographic separation of them. However, these differences are not as distinct as Scholz's illustrations imply (1987) and the geographical separation between them is not as clear-cut as he describes. It is true that the more SW Asian plants have a round callus/scar (Figs. 5.3.1, 6.2.43) and the western ones have an oval one (Figs. 5.3.1, 6.2.45). But in the E Mediterranean both forms co-exist with dominance of the oval type (Fig. 5.3.1). Further, the type specimen of *B. fasciculatus* and some specimens from Cyprus, Libya and the southwest of the

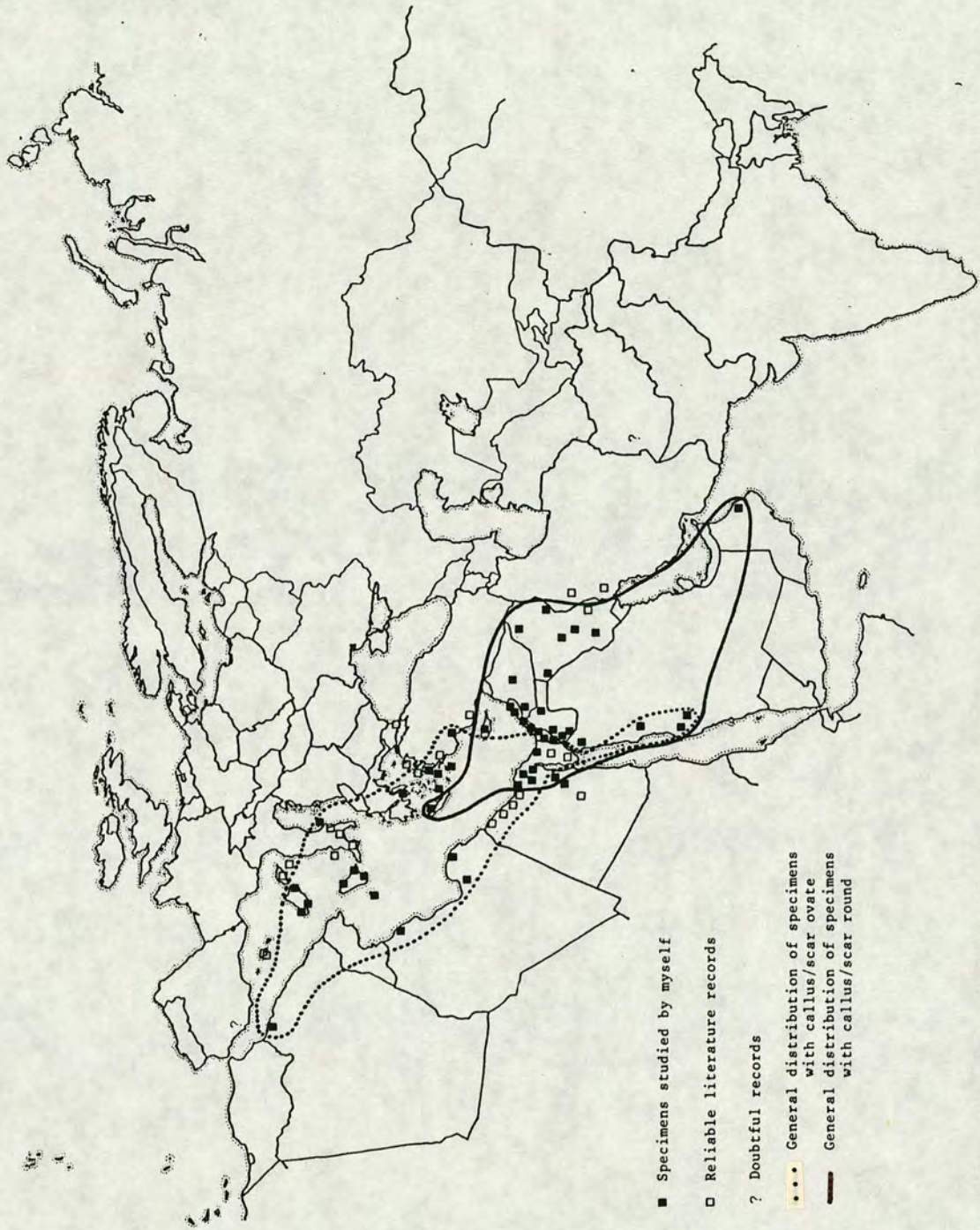


FIG. 5.3.1. Distribution of *B. fasciculatus*. Often each square represents more than 1 gathering. E Mediterranean is the area where both callus/scar forms exist and where populations are particularly abundant.

Arabian Peninsula are of intermediate morphology* (Fig. 6.2.44).

Very rarely the callus is also elliptic** (Fig. 6.2.46).

Despite the geographical connection, the taxonomic significance of the callus/scar shape in *B. fasciculatus* is in no way comparable to the significance of the same character in *B. diandrus/rigidus*. In *diandrus/rigidus* the extreme forms, pointed and oval, are indeed very distinctly different and easily recognisable. The pointed callus can be associated with structural mechanisms for self-pollination and the burial of the grains (see 5.2.3.3) and also often to differences in habitat. But in *B. fasciculatus* the differences of the callus/scar morphology are slight and very difficult to define. The difference between the round and oval shape is so small that it is very unlikely to affect the burial of the grains and the oval callus are not associated with more imbricated spikelets at maturity (self-pollination). In fact, throughout the total range of *B. fasciculatus* the spikelets gradually articulate and diverge from the rachilla axis. In this species this character is merely geographically correlated - a topocline exists - while in *B. diandrus/rigidus* the morphological variations I have found seem to have an adaptive value. In *B. tectorum/lucidus* the morphological variations, discussed in 5.1, apart from having an adaptive value, were strongly geographically correlated - a distinct ecotype

* Greece. Kos, Kos town, *Brenan* 11175 (K); Cyprus: Lakkovaunera forest, *Meiton* 962 (K). Libya: 5km W Baiadas, *Davis* 49954 (K). Jordan: Jebel el'Uweinid, W Azraq, *Townsend* 65/177 (K). Saudi Arabia: Jabal Warjan, 80km SW Madinah, *Collenette* 5225 (K).

** Libya: 30km S Agedabia, *Simpson* 39079 (K). Egypt: Sinai, 111. 1929, *Meinertzhagen* s.n. (K). Israel: Shehumat-Borochoy, 14 III 1933, *Naftolsky* s.n. (K).

exists and consequently I have attributed to it subspecific rank. For a parallel between ecotype and subspecies see Smith (1981). Ecotypic differentiation, which by definition involves genetic adaptation, refers to "any feature of an organism or its parts which is of definite value in allowing that organism to exist under the conditions of the habitat" (Daubenmire, 1959). But in *B. fasciculatus* such a connection cannot be recognized. The variants do not seem to be truly differentiated. Therefore, I disagree with the taxonomic treatment given of Scholz (1987), which gives subspecific rank to these variants. They merit discussion certainly, but not formal taxonomic recognition.

5.4 MULTIACCESS KEY TO THE 6 SPECIES OF SECT. *GENEA*

I found it impossible to construct a normal dichotomising key to the species of *Genea* because of the great morphological variability and overlapping of character states. Different species have several characters in common. As a result of my studies I concluded that the 9 characters used below provide, in combination, the best tool for identification.

Instructions for the use of the multiaccess key:

The characters used in the key are indicated by capital letters (A, B...) and the character states by numbers (A1 & A2; B1 & B2). The character states are:

A 1 Long glumes and lemmas - upper glume 1-47mm long.

2 Shorter glumes and lemmas - upper glume 7.5-1(-21)mm long.

[*B. sterilis* occasionally has upper glumes up to 21mm].

B 1 Rachilla of top sterile florets twisted.

2 Rachilla of top sterile florets not twisted.

C 1 Panicle branches longer than spikelets.

2 Panicle branches shorter than spikelets.

D 1 Panicle branches with few ramifications - up to 2-3.

2 Panicle branches with more ramifications - more than 3.

E 1 Panicle erect.

2 Panicle nodding.

F 1 Glumes and lemmas very narrow - lemma 1.3-1.8mm wide.

2 Glumes and lemmas wider.

G 1 Caryopsides twisted.

2 Caryopsides not twisted.

H 1 Caryopsides straight.

2 Caryopsides outcurved.

I 1 Awns straight.

2 Awns curved.

Thus, the 6 species are defined by the following list of characters states:

B. diandrus - A1, B2, C1 & C2, D1, E1 & E2, F2, G2, H1 and I1.

B. tectorum - A2, B1, C1 & C2, D1 & D2, E1, F2, G2, H1 & H2 and I1.

B. sterilis - A2, B2, C1, D1, E2, F2, G2, H1 & H2 and I1.

B. madritensis - A2, B2, C1 & C2, D2, E1 & D2, F2, G2, H1 & H2 and I1.

B. rubens - A2, B1, C1, D1, E1, F2, G2, H1 and I1.

B. fasciculatus - A2, B2, C2, D1, E1, F1, G1 & G2, H2 & I2.

A table that makes the use of this multiaccess key easier is provided below:

Characters	A	B	C	D	E	F	G	H	I
Taxa									
DI/RI	1	2	1,2	1	1,2	2	2	1	1
TE/LU	2	1	1,2	1,2	1,2	2	2	1,2	1
ST	2	2	1	1	2	2	2	1,2	1
MA	2	2	1,2	2	1,2	2	2	1,2	1
RU	2	1	2	1	1	2	2	1	1
FA	2	2	2	1	1	1	1,2	2	2

CHAPTER 6. MICROMORPHOLOGICAL CHARACTERS

6.1 LEAF ANATOMY

6.1.1 INTRODUCTION

As a result of the work on grass leaf anatomy by W. Brown (1958, 1961), Prat (1960, 1961), Metcalfe (1960) and Jacques-Félix (1962), our knowledge of the systematic significance of leaf characters has greatly improved and their taxonomic value is now generally accepted.

Despite the now extensive literature on the anatomy of grasses, comparative studies are sometimes difficult due to lack of uniformity of definitions and descriptions amongst the different authors. It is, therefore, important to stress the value of Ellis' (1976) descriptive keys and diagrams that standardize and simplify the description of leaf anatomy in the grass family. Material of sect. *Genea* (transverse sections of leaves) was accordingly studied in a search for possible new taxonomic characters. Another reason for studying leaf anatomy in sect. *Genea* was because it might be related to habitat. This relationship could, in turn, reveal some trends in the adaptive radiation of the group. It might also give some indication of the evolution in the section as a whole. If *Genea* is a very recent group it would be surprising if there were many striking differences in the leaf anatomy of its species, in the absence of very notable ecological differences.

Twenty-nine accessions, covering material now recognised as *B. diandrus* var. *diandrus*, and var. *rigidus*, *B. fasciculatus*, *B. madritensis*, *B. rubens*, *B. sterilis*, *B. tectorum* subsp. *tectorum* and subsp. *lucidus* were studied as referred to in Chapter 4.3.

6.1.2 RESULTS

Figures 6.1.1 - 6.1.13 illustrate some of the most relevant features of the leaf anatomy of sect. *Genea* species. Tables 6.1.1 and 6.1.2 list the differences between the taxa recognised.

A description (standardized according to Ellis, 1976), covering the section as a whole, follows and all the anatomical features there described are especially pointed out in Figures 6.1.1 and 6.1.2.

Description of the leaf anatomy in transverse section of sect. *Genea*

General shape in section: Abaxial ribs present as slight undulations associated with the vascular bundles. Adaxial ribs and furrows clearly present. Ribs rounded, situated over all the vascular bundles. All vascular bundles widely spaced, situated at same level in the centre of the blade. Only a single vascular bundle included in the keel. Midrib projecting abaxially and adaxially.

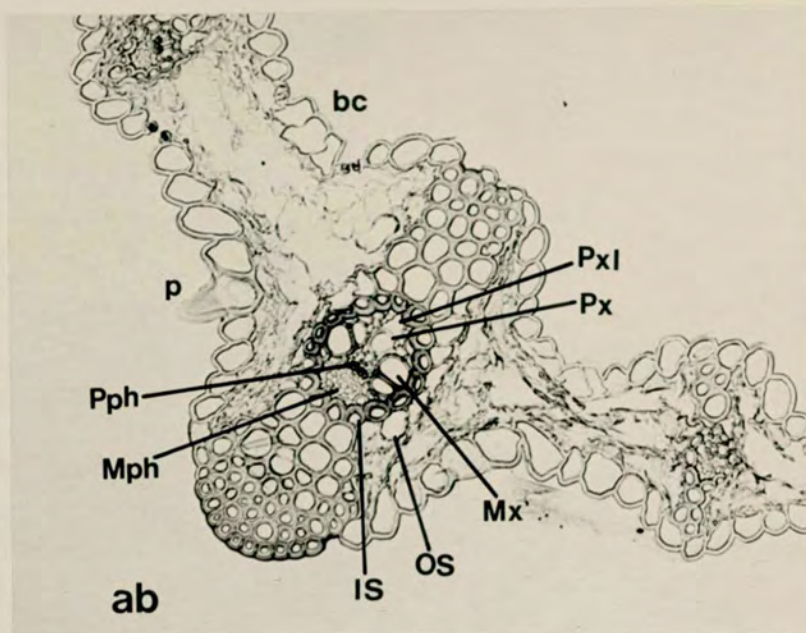
Vascular bundles: Circular or round in outline. Even in third order vascular bundles, xylem and phloem forming distinguishable blocks of tissue first and second order vascular bundle phloem adjoining the inner sheath; protoxylem vessels present; metaxylem vessels circular and very wide (i.e. width of vessels very much more than that of parenchyma sheath cells) and walls distinctly thickened; lysigenous cavities apparently present in all species. Bundle sheath double, inner and outer sheath of numerous (more than 15) circular cells. Inner sheath completely surrounding the bundles. Outer sheath always abaxially interrupted by sclerenchyma fibres; interrupted on both abaxial and adaxial sides on bundles

General legend for Figures 6.1.1 - 6.1.13:

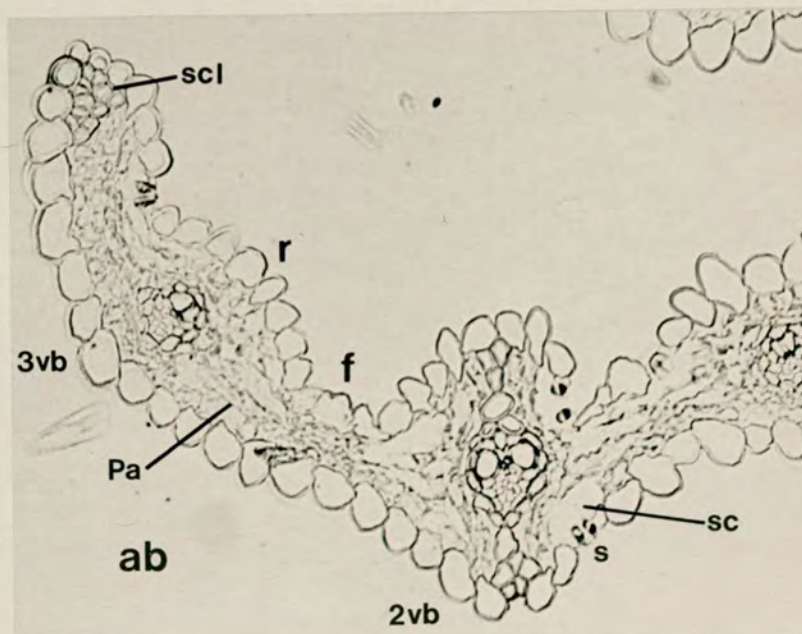
- ab - abaxial surface
- bc - bulliform cells
- ep - epidermis
- f - furrow
- h - hair
- hb - hair base
- IS - inner vascular bundle sheath
- lc - lysigenous cavity
- Mph - metaphloem
- Mx - metaxylem
- OS - outer vascular bundle sheath
- p - prickle
- Pa - parenchyma (chlororeenchyma)
- Ph - phloem
- Pph - protophloem
- Px - protoxylem
- Pxl - protoxylema lacuna
- r - ribs
- s - stoma
- sc - substomatal cavity
- scl - sclerenchyma
- 2vb - 2nd order vascular bundle
- 3vb - 3rd order vascular bundle

FIGURES 6.1.1. and 6.1.2. Leaf anatomy of B. diandrus var. rigidus.

1. Midrib vascular bundle
2. Tip of leaf section.



1

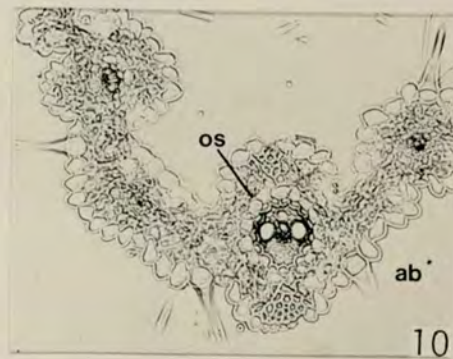
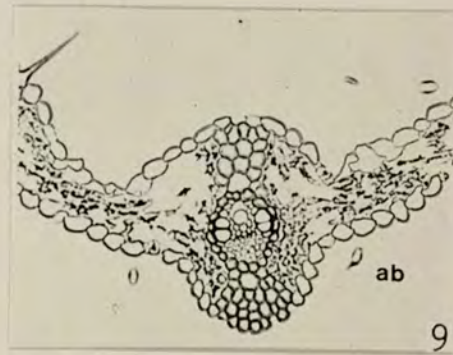
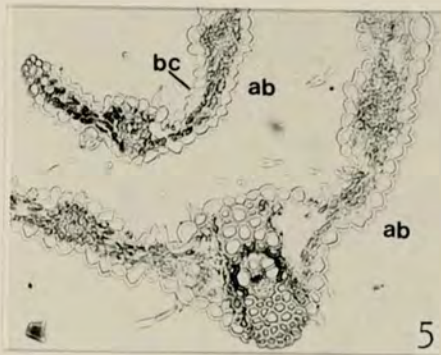
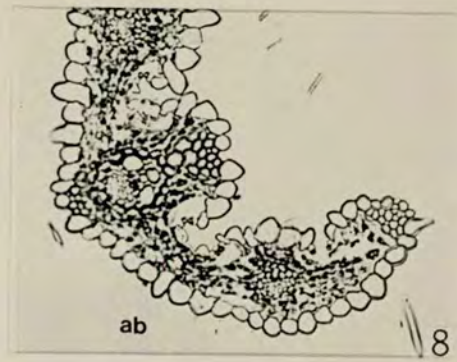
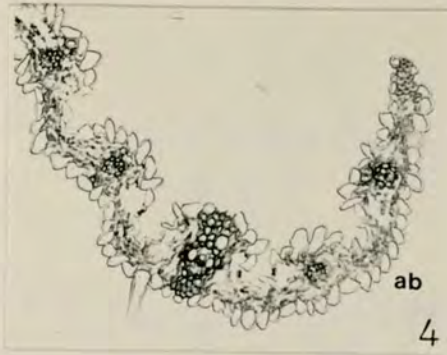
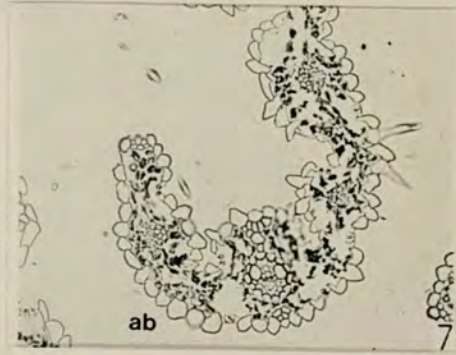
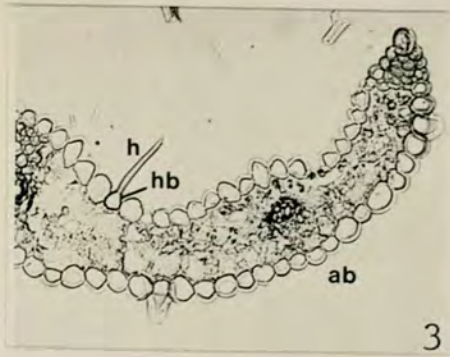


2

— 1μm

FIGURES 6.1.3 to 6.1.10. Leaf anatomy of sect. *Genea* species.
Magnification is the same in all figures.

3. DI. Tip of the leaf section. Note the regular shape of epidermal cells, the wide open furrows and the well preserved chlorenchyma.
4. FA. Tip of the leaf section. Note the pointed sclerenchyma at the leaf tip, the irregular outline of epidermal cells and the narrow and deep furrows.
5. ST. Tip of the leaf section and midrib vascular bundle. Note the broad sclerenchyma at the vascular bundle sheath (especially at the abaxial surface), variable in the *Genea* species. Compare with the narrow one of Figs. 6, 9 and 10.
6. TE. Midrib vascular bundle.
7. TE. Tip of the leaf section. Note the reduced sclerenchyma at leaf tip and the irregular outline of the epidermal cells.
8. LU. Tip of the leaf section. Compare the sclerenchyma at leaf tip with TE, Fig. 7.
9. RU. Midrib vascular bundle.
10. LU. Midrib vascular bundle. Note the narrow sclerenchyma (1 cell) at the vascular bundle on both abaxial and adaxial surfaces. Compare with the broad one on Fig. 5.



— 1 μ m

of second and third order. Inner sheath cells relatively large with all walls thickened, especially the inner wall. Outer sheath cells all similar in size, not markedly larger than the mesophyll cells, with radial walls straight and tangential walls inflated; walls slightly thickened. No sclerenchyma present between the vascular bundles. Sclerenchyma associated with vascular bundles: sclerenchyma formed cells with wide lumina. Well-developed girder of sclerenchyma present on the adaxial side of first order vascular bundles; epidermal cells over girder small and thick-walled; sclerenchyma band as wide or wider than the vascular bundle but narrowing towards the bundle. Well-developed anchor-shaped girder of sclerenchyma present on the abaxial surface of first order vascular bundles; epidermal cells under the girder usually small and thick-walled. Sclerenchyma of second order vascular bundles more or less reduced, absent in bundles of third order. Sclerenchyma in leaf margin: cap-shaped adjoining normal mesophyll cells but not associated with the nearest vascular bundle. Epidermal cells at margin smaller and fibre-like, thickened on all walls; number of normal epidermal cells between the marginal sclerenchyma and nearest bundle rather uniform in all species (7 epidermal cells).

Chlorenchyma: U-shaped occupying the sides and bases of furrows, not radiate.

Epidermis (except as otherwise noted above): Outer tangential wall of each epidermal cell thickened individually; cuticle not seen but wax covers the epidermis as observed by SEM (Chapter 6.2, Fig. 6.2.13); epidermal cells of variable form, often slightly arched externally or expanded into papillae and prickles. Groups of

bulliform cells \pm conspicuous, often present at the base of furrows on the adaxial surface. Macro-hairs with bases sunk in the epidermis. Stomata somewhat below the level of epidermal cells, more numerous on adaxial surface, located on both sides of the furrows, near the vascular bundles.

6.1.3 DISCUSSION AND CONCLUSIONS

As referred to in Chapter 4.3 (Material and Methods), anatomical sections were made using herbarium material; only a few observations were made with fresh hand-cut sections. Leaves of dried specimens are a good, ready-to-use, source of material for anatomical studies, but the degree of cell-collapse to be expected is higher than when fresh material is used. The cells of the mesophyll with thinner cell walls and those of the outer bundle sheath can both totally collapse. Furthermore, the preservation of tissues depends on the conditions under which the plants were dried. In a comparative study, allowances have to be made for this. I had some success with a pre-treatment of the herbarium material with detergent (see Chapter 4.3) which restored the cells to their original shape. In some cases, this process was more successful (Fig. 6.1.7) than in others (Fig. 6.1.1). However, the strikingly irregular shapes and sizes of epidermal cells (e.g. Fig. 6.1.4) seem not to be due to artefacts of technique and were constantly observed in the same taxon.

The differences in the leaf anatomy in *Genea* as observed in different specimens of each taxon were very small. For this reason, I thought it was not worthwhile looking at more than the 3 accessions of each.

Due to lack of clear-cut anatomical diagnostic features, leaf anatomy is not of much use for species circumscription in this group. Although it may provide some understanding of the evolution and biology of these plants (see Chapter 9) other features than leaf anatomy have to be relied upon for taxonomic purposes.

The most relevant differences in leaf anatomy can be related to environmental conditions. The amount of water available to a plant and the light/shade balance are among the factors that ultimately determine, via natural selection, the most significant differences in leaf anatomy. The parts of grass leaves most affected by them are: the inrolling of the leaf, the shape of furrows and ribs, the number and position of stomata on both surfaces, the thickness of epidermal cell walls, and the presence/non-presence of \pm thick cuticle and of superficial sclerenchyma. Inrolled surface, deep and narrow furrows, few stomata sunk in the epidermis, located at the base of furrows, thick epidermal cell walls and thick cuticles are all likely adaptations to reduce the loss of water. A dense indumentum can also reduce the amount of water lost by transpiration, but I have observed in this group that different degrees of pubescence are distributed randomly throughout the geographic range of species.

The general ability that most *Genea* species seem to have for growing almost anywhere in temperate and semi-desert areas is mirrored by the small interspecific differentiation of the leaf anatomy. However, some anatomical characteristics may be related to ecological preferences.

Although the general question of the relation between leaf

anatomy, ecology and the biology of *Genea* is addressed in some detail in the chapter on adaptive radiation (Chapter 9), it is appropriate here to make some specific observations on this subject.

B. tectorum subsp. *lucidus* is restricted to SW Asia, growing in quite dry places, even semi-deserts. Under the artificial conditions of the Edinburgh glass-house it never survived to complete its life cycle. *B. fasciculatus*, although not showing such extreme requirements, is another species of very dry, hot places. *B. rubens* and *B. diandrus* var. *rigidus* usually grow in places where there is not much water available. *B. madritensis* and *B. diandrus* var. *diandrus* are plants of open ground, but in the wild can grow also in semi-shady places. In contrast, *B. sterilis* is typically a species of temperate areas, common in C and N Europe.

The leaf anatomy results reveal that deeper and narrower furrows are, in *Genea*, more associated with dry habitats, as is to be expected (Table 6.1.1). *B. sterilis* has a quite high number of stomata per unit area of lamina (9.47). In contrast, *B. tectorum* subsp. *lucidus* (from very dry places) has an even higher number (10.29, the highest number in *Genea*) while *B. fasciculatus* has a lower one (8.43). *B. diandrus* var. *diandrus* has the lowest value (4.55).

The ratio "number of stomata on adaxial surface/number of stomata on abaxial surface" also seems to be very interesting. Because of the often strong undulations (furrows and ribs) on the adaxial surface plus the slightly involute blades, the abaxial

TABLE 6.1.1 List of the significant differences in the leaf anatomy of sect. *Genea* species. The character states here described are illustrated in Figures 6.1.1-6.1.10.

	DI	FA	MA	RI	RU	LU	ST	TE
Slight, shallow furrows, i.e. less than a quarter of the leaf thickness	X		X	X	X			
Medium furrows, i.e. a quarter to one half the leaf thickness		X		X		X	X	X
Wide open furrows, i.e. obtuse angle formed by furrow sides at base	X		X	X	X	X	X	
Narrow furrow, i.e. sides of furrow almost vertical; base fairly broad but sides steep		X		X		X		X
Sclerenchyma cap in leaf margin round				X		X		X
Sclerenchyma cap in leaf margin pointed	X	X	X	X	X		X	
Sclerenchyma cap in leaf margin narrow, very pointed projection		X						
1st bundle at margin with sclerenchyma		X		X			X	
1st bundle at margin without sclerenchyma	X		X		X	X		X

surface can be more exposed to the environment than the adaxial and so the differences of stomata number probably represent some physiologically effective, advantageous differentiation. The ratio mentioned above is indicated for each taxon in Table 6.1.2. The higher the ratio the bigger the difference between the number of stomata on both surfaces (there are fewer stomata on the adaxial surface). The closer the ratio to 1 the more similar are the numbers of stomata of both surfaces; below 1 it means that the abaxial surface has more stomata than the adaxial. *B. sterilis* is clearly separated from all the other *Genea* species by having a very high ratio (4.18, Table 6.1.2). The mechanism of differentiation in the remaining species seems to have followed 2 distinct (even opposite) strategies. In fact, both *B. fasciculatus* and *B. tectorum* subsp. *lucidus* which live in the most dry conditions present the extremes of this ratio (2.62 and 0.97 respectively). While in the first the plants protect themselves from desiccation by having the combination of inrolled leaves and very few stomata on the abaxial surface, in *B. tectorum* subsp. *lucidus* the plants seem to be prepared to lose a reasonable amount of water by transpiration. It is important here to remember that transpiration cools the leaves and can be an important factor for survival in hot climates. In *B. tectorum* subsp. *lucidus* the adaptation, contradictory at first sight, seems to be the same as that described in detail for *B. rubens* by Killian (1942). This botanist studied specimens of *B. rubens* from semi-desertic places in N Africa regarding their ecology. He noticed that this species does not present the usual adaptations that prevent the loss of water by transpiration (e.g. reduction of parts, few stomata,

TABLE 6.1.2 Mean leaf stomata numbers in *Genea* species: ratios on adaxial and abaxial surfaces and number of stomata per unit area. Stomata were counted in 20 sections as each accession used and averages were calculated.

Taxon	Mean no. stomata on adaxial surface (X)	Mean no. stomata on abaxial surface (Y)	Ratio X : Y
ST	14.2	3.4	4.18
FA	11.8	4.5	2.62
MA	14.1	6.3	2.22
RU	16.3	8.6	1.90
RI	22.0	12.5	1.76
DI	13.2	10.0	1.32
TE	15.4	12.2	1.26
LU	17.5	18.0	0.97

stomata sunk in the epidermis or succulence). It is in all respects a typical plant of shade. The much-developed root system protected by a mucilaginous sheath can absorb a great amount of water of condensation from the loose sandy soil when the osmotic pressure is high - which is the case because these plants lose quite a lot of water by transpiration.

Furthermore, it seems that there is a strong correlation between the groups of taxa formed according to the ratio "number of stomata on adaxial surface of lamina/number of stomata on abaxial surface" (Table 6.1) and the groups of taxa defined by the external morphology (see Chapter 5). An interpretation of these correlations in terms of adaptive radiation is provided in Chapter 9.

6.2 SURFACE CHARACTERS AS SHOWN BY SCANNING ELECTRONIC MICROSCOPY (SEM)

6.2.1 INTRODUCTION

Characters of leaf epidermis have been much used in grass taxonomy (e.g. Davies, 1959; Gould, 1968; Metcalfe, 1960; Slade, 1970; Stace, 1965). The great morphological variation in the different kinds and forms of epidermal cells in this family sometimes provides good taxonomic characters, and have been used in tribal and subfamily delimitation. These cells - long cells, short cells, prickly hairs, micro-hairs, macro-hairs - can have different shapes and sizes. Throughout the family, they can be variously distributed in the leaves in the costal zones (opposite to the veins) and the intercostal zones (in between the veins). There are also differences when abaxial and adaxial surfaces are

considered and when the epidermis of different organs is compared.

The present investigation of the micro-surface of different organs in sect. *Genea* using scanning electronic microscope (SEM) had 2 components: (1) the surfaces of leaves, pedicels, lemmas, paleas, lodicules, grains and awns were studied in order to provide a description of their epidermis and to establish possible distinctive, taxonomically relevant characteristics; (2) the surface of certain parts of the plants was also investigated from a form and function point of view - where this seemed relevant in understanding the biology and special adaptations of particular taxa (e.g. the development of the callus at the base of the floret related to the disarticulation of the spikelet, presence of stomata on awns, etc.).

The materials and methods used are described in Chapter 4.

6.2.2 RESULTS

The differences between species as revealed by SEM are indicated in Table 6.2.1. Descriptions of the epidermis of different organs, notes on particular features and their relation to its function, together with relevant illustrations, follow.

6.2.2.1 General description of epidermis and notes on particular features

A description of the epidermal cells in *Genea* follows. Because I did not find any major variation amongst the species I decided to describe the different kinds of cells throughout the parts of the plants studied instead of the various organs separately. Descriptions are standardized according to Ellis

TABLE 6.2.1 Micromorphological analysis of the SEM results. Ab - Abaxial surface; Ad - Adaxial surface. Numbers in circles refer to figures illustrated in this Chapter.

CHARACTERS/ CHARACTER STATE			DI		FA		MA		RI		RU		SE		ST		TE	
			Ab	Ad	Ab	Ad	Ab	Ad	Ab	Ad	Ab	Ad	Ab	Ad	Ab	Ad	Ab	Ad
Sheath	Stomata		Yes	Yes	Yes	Yes	Yes	Yes	Yes	No	Yes	Yes	Yes	No	Yes	Yes	Yes	No
	Silica bodies		Yes	No	No	No	Yes	No	?	No	Yes	No	Yes	No	Yes	No	Yes	No
Leaf blade	Hairs distribution		Everywhere	Ribs	Ribs	Everywhere	Everywhere	Everywhere	Ribs	Everywhere	Ribs	Everywhere	Ribs	Everywhere	Ribs	Everywhere	Ribs	Everywhere
	Silica bodies		Present	Present	Absent	Absent	Absent	Present	Present	Present	Present	Present	Absent	Present	Present	Present	Present	?
		Outline	Undulate	Straight	-	-	-	Slightly undulate	Straight	Straight	Straight	Straight	-	-	Undulate	Undulate	Undulate	Undulate
		No.	Many	Few	-	-	-		Many	Many	Few		-	-	Undulate	Undulate	Undulate	Undulate
	Hairs (H) & prickles (P) along the edge			P		P		P		P		P		H		P		H
*Lemma	Short cells	No.prickles	11	-	44	-	32	-	20	-	?	-	9	-	30	-	18	-
		No.silica bodies	6	-	13	-	14	-	11	-	?	-	3	-	2	-	5	-
Awn stomata			Yes	Yes	?	No	Yes	No	?	-	Yes	No	Yes	Yes	Yes	No	?	No
Palea hairiness	Nerves	Range of variation	Discontinuous variation		Discontinuous variation		Discontinuous variation		Discontinuous variation		Discontinuous variation		-		Continuous variation		Continuous variation	
		Posture	Erect		Erect		Erect		Erect		Erect & Patent		-		Erect		Irregular	

* Cells counted on a SEM micrograph taken at the magnification of x500-561.

(1979).

Long cells

Long cells constitute most of the epidermal surface of all organs and have a constant, or relatively constant, shape and size in any particular organ. Long cells are elongated (3x or more than their width) with side walls parallel to each other and end walls at right angles to the horizontal walls, sometimes slightly angled or rounded, especially on the leaves, or sloping in relation to the horizontal walls (Figs 6.2.1; 8; 11; 12; 13; 17). Cell wall straight, not undulate on the leaf blade, adaxial surface or leaf-sheath, on the base and the top of the paleas, hyaline margins of lemmas, adaxial surface of lemmas, on the top portion of awns but more rarely at the base on the adaxial surface of the awns (Figs 6.2.1; 2; 3; 5; 6; 8; 9; 10; 18; 19; 20); deeply Ω -undulating, strongly corrugated on the lemma, middle portion of the palea, base of the awn, sometimes the rachilla and the pedicel (Figs. 6.2.7; 9; 11; 12; 13; 17; 21; 34). All epidermal cells are in general much smaller in *B. fasciculatus*. This is particularly evident in lemmas (Fig. 6.2.14).

Short cells

These I define as all cells smaller than the average intercostal long cells. Cells of the stomatal complexes, cells of the base of prickle-hair and macro-hairs are also short cells, but are described separately.

Silica cells: Cells with silica bodies; circular, elliptic or \pm half-moon as seen in surface view (Figs. 6.2.1; 4; 7; 10; 11; 12; 13).

Cells with papillae: Papillae are convex or conical

projections on the surface of epidermal cells. In *Genea*, papillae are present only in short cells. There is 1 papilla per cell, centrally positioned, circular or rounded at base as seen in surface view, conical, thick-walled; all papillae point to the apex of the organ, but not over-arching neighbouring cells (Figs. 6.2.7; 9; 11; 12; 13; 14).

Both silica cells and cells with papillae may be solitary (Figs. 6.2.1; 7; 9; 13) or in pairs beside each other (Figs. 6.2.11; 12), situated between each successive long cell in a file (Figs. 6.2.7; 9; 11) or, more rarely, pairs of long cells in a file; they are especially common in lemmas (but not on the hyaline margin - Fig. 6.2.9), paleas and rachilla (Figs. 6.2.34; 38; 40; 42; 43; 45; 54). Papillae cells are absent on the leaves, but silica cells can be present on the midrib on both leaf surfaces. Silica cells on leaves have smooth or undulated outlines (Figs. 6.2.1; 4); whereas on the other organs, both silica cells and papillae cells have deep Ω -undulating, strongly corrugated cell walls (Figs. 6.2.7; 12).

Stomata

Stomatal complexes are long and narrow with parallel-sided subsidiary cells (Figs. 6.2.1; 5; 10; 11; 12; 16; 17). Often 1 interstomatal long cell lies in between the stomata (Fig. 6.2.11). Stomata are present: on both surfaces of the blades beside the costal zones; on both surfaces of leaf-sheaths, although only a few on the adaxial surface; and on both surfaces of lemmas and awns and along the 2 veins of paleas.

Prickle hairs

Prickles are cells with swollen bases and short, sharp

spines or barbs. These structures are the cause of the rough texture of an organ. In *Genea* the base of the prickles is large (\pm twice as long as the stomata); the spine is usually long, about the length of the base always pointing towards the apex of the organ. Prickles sometimes occur on the leaf margin (Fig. 6.2.2) and always on lemmas (Figs. 6.2.12; 45) and along the awns (Figs. 6.2.15; 16; 18; 19; 20). The awn terminates with prickle-hairs which diverge at the apex (Fig. 6.2.20).

Macro-hairs (micro-hairs are absent in *Genea*)

Macro-hairs are unicellular with no specialized cells associated with its base. Their bases are superficial, swollen in relation to the hair thickness (Figs. 6.2.2; 3), and of variable length and frequency.

Macro-hairs on paleas:

The variation of the hairiness on the 2 veins of paleas in *Genea* involves the number and length of hairs. The variation within a species is typically great and is of the same order as the general hairiness of the whole plant - which is taxonomically useless - as I have discussed in the taxonomic section of the thesis. Despite these limitations, it is still possible to recognize some basic kinds of hairiness on palea nerves. *B. tectorum* is readily distinguished by its longer, more spread out and often collapsed spiral hairs (Figs. 6.2.27; 28). In most of the other species the hairs are \pm long, \pm spreading, more clearly spaced out and with very small hairs in between them (Figs. 6.2.22; 23; 24); an exception is *B. fasciculatus* with hairs extremely short and *B. diandrus* var. *diandrus* without small hairs in between the longer ones that are typically rigid, ascending,

well spaced and larger at their base.

The adaxial surface of the palea is always glabrous. The abaxial surface can be glabrous (Fig. 6.2.24), with very sparse hairs (Fig. 6.2.26) or very hairy (Figs. 6.2.22; 23; 28). One single species can exhibit the whole range of this variation.

Wax

Both leaf epidermis, and the abaxial epidermis of lemmas is covered with wax (Fig. 6.2.1; 4; 13).

Ligule

All *Genea* species have membranous, smooth ligule surfaces with no signs of vascularization as reported for *B. sterilis* by Chaffey (1985) (Fig. 6.2.30).

Lodicules

There are 2 very thin hyaline lodicules inserted at the palea base surrounding the ovary and later the grain (Fig. 6.2.31). As in the ligule, their surface is membranous and smooth, without stomata or any kind of specialized cells (Fig. 6.2.32).

Shape of awns

The adaxial surface of the awns is concave nearer the base (Fig. 6.2.14) and sometimes the edges of the awn inroll over this surface (Fig. 6.2.18). The awn becomes terete towards the apex (Figs. 6.2.19; 20).

Vascular bundles along the rachilla

Although this is an "anatomical feature" it was well observed in SEM and therefore is discussed here. The number of vascular bundles along the rachilla at the level of the fertile florets seems to be consistently 3. These vascular bundles are clearly observed at the base of the second floret, at the scar

area (Figs. 6.2.51; 54), at the top of the rachilla segment of the second floret (Fig. 6.2.61). They are also observed at the level of the third floret.

6.2.2.2 Form and function: a SEM investigation

Development of callus/scar

The disarticulation of the spikelets by separation of the florets that are, thus, dispersed individually, is due to the existence of a fully developed callus below each rachilla segment (internode). SEM is ideal for showing the presence or absence of a fully developed callus. The callus morphology is the external manifestation of an abscission layer, below a floret.

In *Genea* the fertile florets in a spikelet disarticulate and disperse separately due to the full formation of a callus that surrounds the whole of the lemma base (Figs. 6.2.33; 34). The sterile florets disperse together with the uppermost fertile one because on these the points of spikelet-articulation along the rachilla have an incomplete callus, indeed a non-existent one in the uppermost sterile floret (Figs. 6.2.36; 37). The only exception is *B. tectorum* subsp. *lucidus* where all the spikelets are dispersed together. In these plants a fully-developed callus is formed only below the basal floret. All the other points of floret-articulation along the rachilla have an incomplete callus (Figs. 6.2.38; 40). The importance of this difference in adaptative terms and its taxonomic consequence are discussed in Chapters 5.2; 5.3 and 9.

Callus and scar shape

There is some variation in the shape of the callus and the scar at the lemma base within a single spikelet and for this

reason I have standardized my observations by always referring to the callus/scar of the second floret from the base*. There is also a continuous variation in both callus and scar shape among the taxa in *Genea*. The scar is most often obovoid (*B. diandrus* var. *diandrus*, *B. fasciculatus*, *B. madritensis*, *B. rubens*, *B. tectorum* (Figs. 6.2.50; 44; 41; 42; 35)) or circular (*B. fasciculatus*, *B. sterilis* (Figs. 6.2.43; 52)), but it can also be \pm elliptic (*B. diandrus* var. *rigidus*, *B. diandrus* var. *diandrus* and *B. fasciculatus* (Figs. 6.2.47; 49; 46)). This character has been used by some taxonomists for the delimitation of some taxa. Largely for this reason *B. rigidus* has been separated from *B. diandrus* (see Chapter 5.2) and Scholz (1987) recognized 2 subspecies in *B. fasciculatus* essentially on the callus shape character (see Chapter 5.3). However, as I have observed, there is no clear-cut division between the different shapes of the scar in either example cited above: the number of forms intermediate between *B. sterilis*, *B. diandrus* var. *diandrus* and *B. diandrus* var. *rigidus* is great (Figs. 6.2.47-54). For this reason, and in spite of the specialisation that a particular form might represent (e.g. the elliptic scar in *B. diandrus* var. *rigidus* probably plays an important role in dispersal and burial of the grain) I do not consider this particular feature of major taxonomic importance, at least at the present evolutionary stage of the species of *Genea*. This is discussed in greater lengths in Chapters 5 and 9.

* It is possible that in some ways the insertion of the first floret is related to the insertion of the glumes and if that is the case we would be analysing more than 1 character at the same time; the uppermost florets are sterile and usually the shape of the callus/scar is atypical.

The callus that surrounds this scar may be \pm rounded (Figs. 6.2.42; 54) to quite pointed (Fig. 6.2.47).

Particular features at the lemma base

As discussed in greater detail in Chapter 5.2.3.3, the back of lemma is either straight or strongly constricted at the base (Figs. 6.2.55; 56), possibly playing an important role in the disarticulation of the spikelet of *B. diandrus* and, therefore, in its dispersal biology.

The longer, stiffly erect hairs at the sides of the callus/scar area, even in generally less hairy specimens, may well facilitate the anchorage and burial of the grain (Figs. 6.2.41; 44; 54; 56).

Stomata on awns

The existence of functional photosynthetic tissue in the awns of annual grasses has been discussed by Grundbacher (1963) and Smith (1991). I have observed open, possibly functional, stomata in the awns of *Genea* species (Figs. 6.2.16; 17). The number of stomata was variable in a species and although my observations in this respect were not very extensive I concluded that *B. diandrus* var. *diandrus* has a higher number of stomata on the adaxial surface than the other *Genea* species.

The transference of photosynthetic function from leaves, stems and lemmas to the awns towards the end of the life-cycle, when most of the plant photosynthetic tissue is dead or may be ineffective, can have an important role in the complete formation of the grains (cf. Grundbacher, 1963).

Adhesion of the anthoecium to the grain

As in some other grasses (e.g. *Festuca*, P.M. Smith - pers.

comm.) there has been reported for some *Bromus* species the existence of a substance that strongly glues both the lemma and the palea to the grain (Smith, 1989). This substance is possibly pectin and is chemically destroyed by the action of EDTA (ethylenediaminetetra-acetic acid). I observed the existence of this glueing mechanism in all *Genea* species. An indication of its power is the need for hydrolysis in 50% sulphuric acid, during dehusking when plant material (grains) had to be prepared for protein extraction (Chapters 4 and 7). An attempt to free the grains from lemmas and paleas results in the destruction of the lemma and palea epidermis and the outer pericarp (Figs. 6.2.57; 58). The most obvious functions of this substance are to ensure mechanical protection of the grain by the lemma and palea and the attachment of the grain to its dispersal apparatus formed by the lemma, awn, palea and rachilla segment.

"Articulation" tissue in the leaf

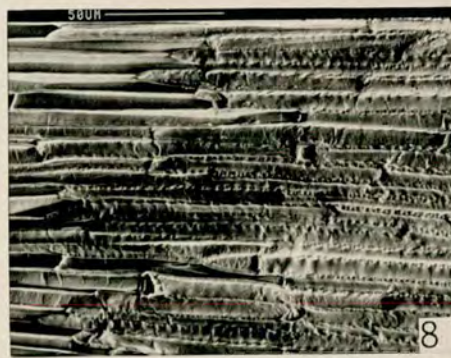
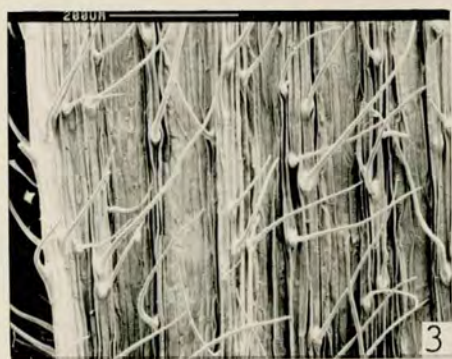
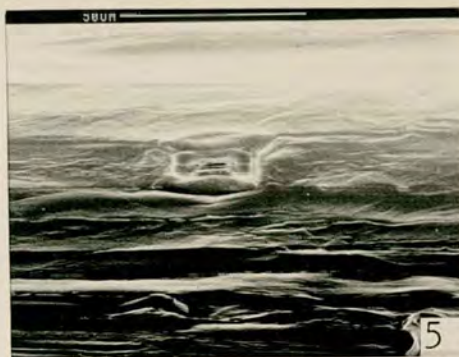
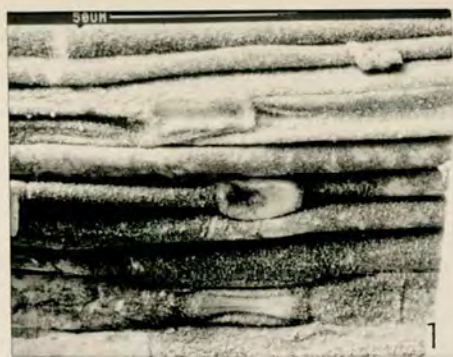
It seems that in some cases there is a tissue differentiation between the leaf sheath and blade, at the ligule level. The epidermis in this area can be smoother and cells less inflated (Fig. 6.2.59) or strongly wrinkled (Fig. 6.2.60). It is possible that this zone is involved in some kind of hydraulic movements of the blade in relation to the sheath. Varying water potential of this tissue may induce movements of the leaf blade to adjust to the optimal exposure to temperature and desiccation. The functions and structure of this area, and of the auricles which it sometimes features, are incompletely known and deserve more attention from physiologists.

6.2.3 CONCLUSIONS

Apart from the callus results, the most significant finding in this SEM research is that there are no major epidermal features that characterize individual *Genea* species. This lack of differentiation agrees with my anatomical observations that, despite ecological distinctions, *Genea* species are very similar to each other, morphologically, and the processes of speciation may not yet be complete. The analysis of these findings in terms of adaptive radiation are discussed in greater length in Chapter 9.

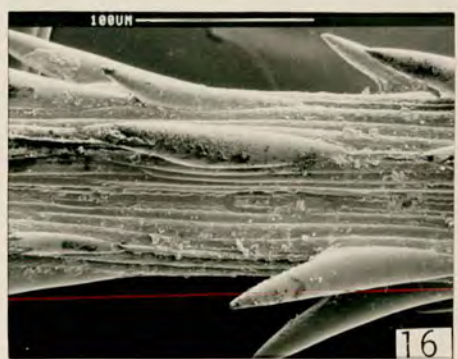
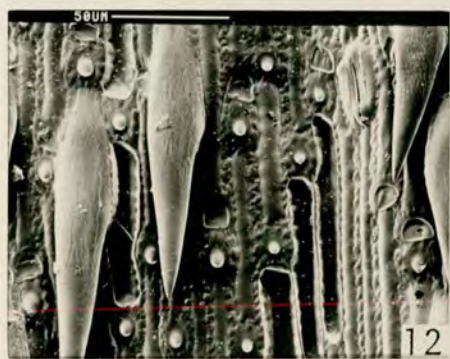
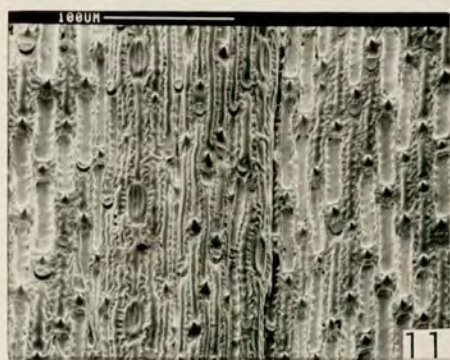
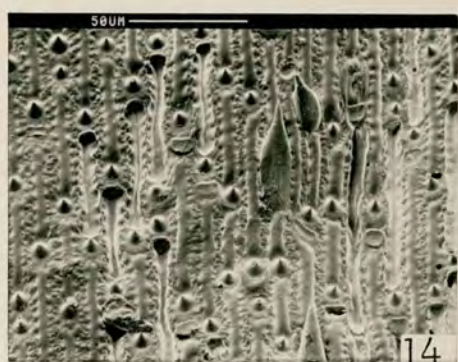
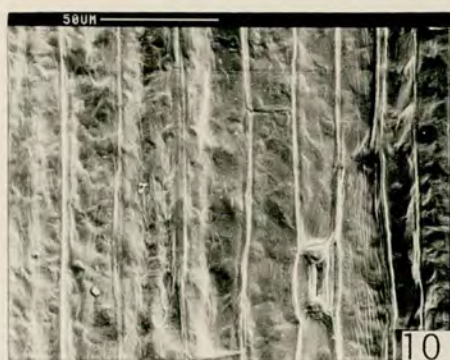
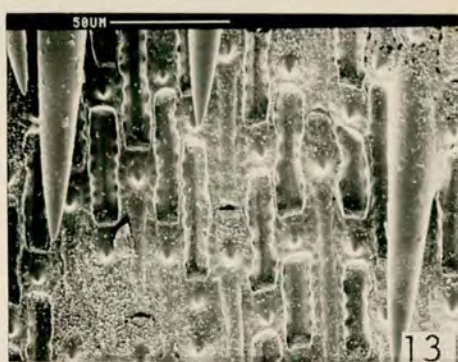
FIGURES 6.2.1 to 6.2.8. SEMs of sect. *Genea* species; magnifications are indicated by bars.

1. RU. Abaxial surface of leaf blade.
2. RI. Abaxial surface of leaf blade with prickly hairs along the margin and macro-hairs on the surface.
3. TE. Abaxial surface of leaf blade with macro-hairs along the margin and surface.
4. ST. Abaxial surface of leaf blade. Note the markedly undulate margin of epidermal cells.
5. FA. Adaxial surface of sheath. Note the open (? functional) stomata.
6. ST. Abaxial surface of palea basal portion. Note the transition from straight (at base, right-hand side) to corrugated cell walls.
7. ST. Abaxial surface of palea middle portion. Note short cells (papillae and silica cells) in between each long cell. Short cells are isolated or in pairs.
8. ST. Abaxial surface of palea top portion. Note the transition from corrugated to straight cell walls towards the apex (left-hand side).



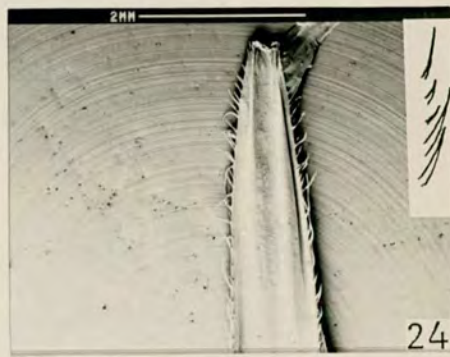
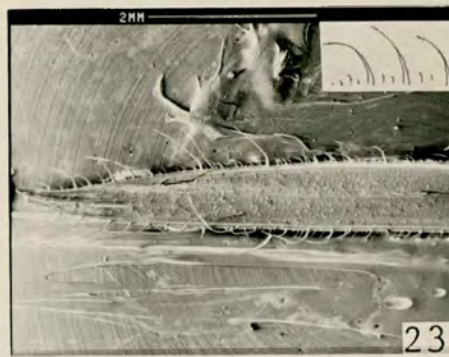
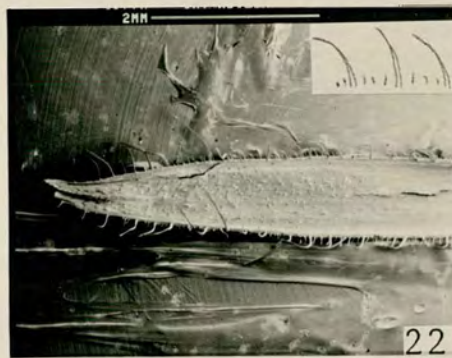
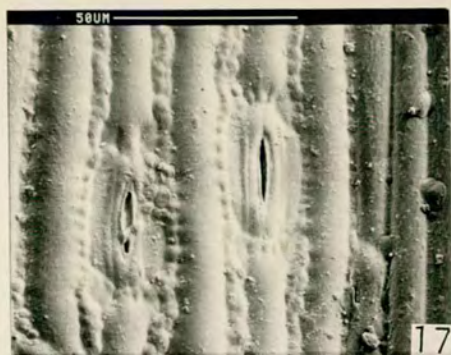
FIGURES 6.2.9 to 6.2.16. SEMs of sect *Genea* species; magnifications are indicated by bars.

9. DI. Abaxial surface of lemma. Hyaline margin (to the right) has no short cells and the long cells have straight walls.
10. MA. Adaxial surface of lemma. Note the open (? functional) stomata and long cells end walls at right angles with the horizontal walls.
11. TE. Abaxial surface of lemma. Note stomata separated by 1 long cell on the midrib and the numerous short cells, isolated or in pairs.
12. RI. Abaxial surface of lemma. Note the short cells isolated or in pairs. All cells (including short cells) have corrugated margins.
13. ST. Abaxial surface of lemma. Note the abundant waxy material that covers the epidermis.
14. FA. Abaxial surface of lemma. Note the very smaller size of cells compared with Figs. 11-13.
15. MA. Concave adaxial surface of awn ("*in setam canaliculatam desinens*" Dumortier 1823 - see Chapter 4.1.4).
16. LU. Adaxial surface of awn. Note the single row of stomata.



FIGURES 6.2.17 to 6.2.24. SEMs of sect. *Genea* species; magnifications are indicated by bars.

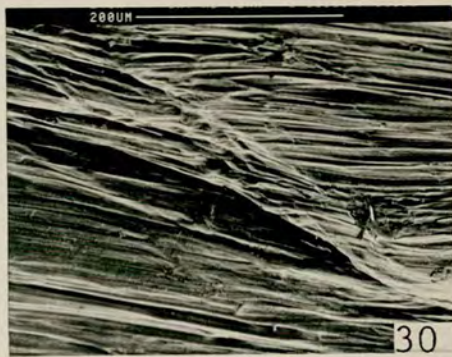
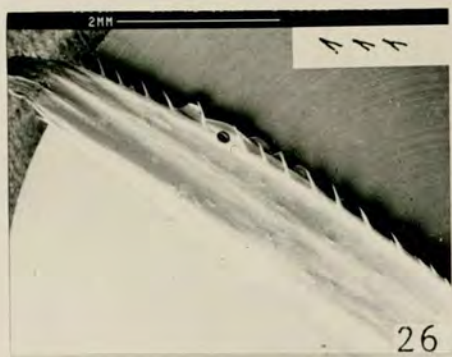
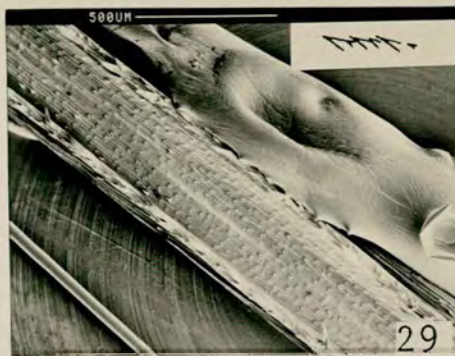
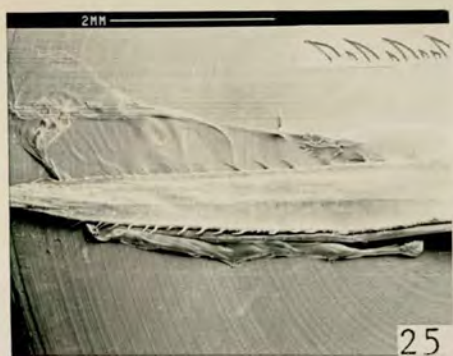
17. DI. Stomata on the adaxial surface of awn. Stomata are open (? functional).
18. RI. Adaxial surface of awn at base. The awn is inrolled over its adaxial surface. Note the robust, long-based, prickly hairs.
19. RI. Adaxial surface of awn, middle portion. In *Genea* the awn is always terete from the middle portion to the top.
20. ST. Awn, topmost portion. Note that the awn on its upper part is exclusively formed by prickly hairs.
21. RU. Top of pedicel. Note the strongly corrugate epidermal cells. N.B. the uncertainty of the glume insertion position.
22. RI. Abaxial surface of palea and interpretative drawing of hairs at margins. Numerous short hairs on the surface.
23. RU. Abaxial surface of palea and interpretative drawing of hairs at margins. Numerous short hairs on the surface.
24. ST. Abaxial surface of palea and interpretative drawing of hairs at margins. The surface is glabrous.



FIGURES 6.2.25 to 6.2.32. SEMs of sect. *Genea* species; magnifications are indicated by bars.

25. MA. Abaxial surface of palea and interpretative drawing of hairs at margins. The surface is glabrous.
26. DI. Abaxial surface of palea and interpretative drawing of hairs at margins. The surface has very few hairs.
27. ^{*}TE. Abaxial surface of palea and interpretative drawing of hairs at margins. The surface is glabrous and has numerous papillae cells. Note that the hair structure has resulted in collapse and spiralling of the cell.
28. ^{*}LU. Abaxial surface of palea and interpretative drawing of hairs at margins. The surface has numerous long hairs. Note that the hair structure has resulted in collapse and spiralling of the cell.
29. FA. Abaxial surface of palea and interpretative drawing of hairs at margins. Note the very short hairs. The surface has numerous papillae cells and prickly hairs.
30. FA. Adaxial surface of ligule. Note the straight cell walls (similar to the lodicules, Fig. 32) and base (Fig. 6) and top (Fig. 8) of palea.
31. DI. Palea and lodicules enveloping the caryopsides. Note how the lodicules are attached to the palea at their base (entirely free from the lemma) and envelope the base of the grain.
32. FA. Abaxial surface of lodicule. Note the straight cell walls (similar to the ligule, Fig. 30).

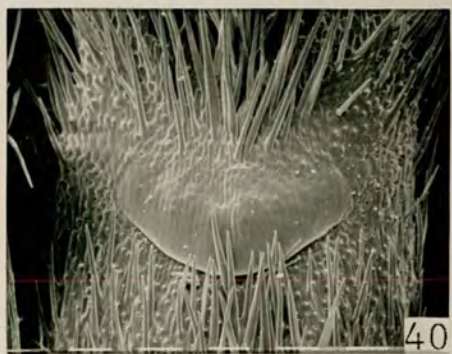
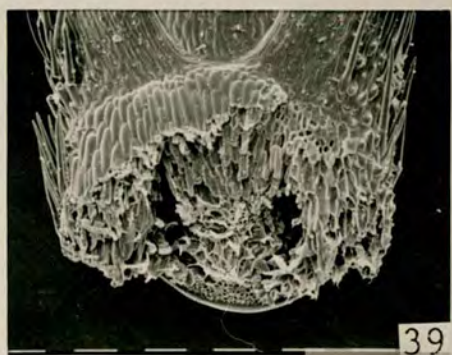
* bar = 1000 μ m



FIGURES 6.2.33 to 6.2.40. SEMs of the sect. *Genea* species; magnifications are indicated by bars.

- 33.* TE. Base of 2nd floret connected with the rachilla segment below. Note the horizontal line of abscission (callus) between the rachilla and the floret shown in detail on Fig. 34 (chorispermous plants). Compare with Fig. 38, synaptospermous plants.
- 34.* TE. Callus area: junction of the 2nd floret with the rachilla segment below. The callus area at the base of the floret has a totally smooth surface and the place of floret abscission is along the diagonal line. Note the strongly corrugated cell walls on the floret base.
- 35.* TE. Base of 2nd floret: callus/scar area. Note the circular, smooth ring area of abscission around the scar (chorispermous plants).
36. TE. Top sterile florets. Note the curved rachilla segments that make the sterile florets spread out.
37. TE. Top sterile florets (detail of Fig. 36). Note the curved rachilla segment and the absence of a callus area at the base of the sterile floret on the left-hand side.
- 38.* LU. Base of 2nd floret connected with the rachilla segment below. Note the uninterrupted epidermis between the rachilla (left-hand side) and floret (right-hand side) consequence of an only partially developed callus between the two (synaptospermous plants).
- 39.* LU. Base of 2nd floret: callus/scar area. Note the smooth small area at the floret base and the abundant tissue around the scar when breakage between floret and rachilla is forced; all indicating only a partially developed callus at the floret base (synaptospermous plants).
- 40.* LU. Base of 3rd floret connected with rachilla segment below. Note the clearly incomplete callus formed between rachilla and floret (synaptospermous plants).

* bar = 100 μ m



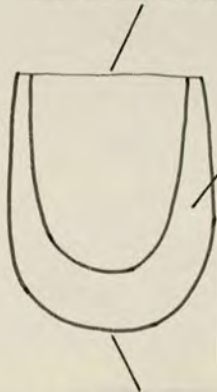
FIGURES 6.2.41 to 6.2.46. SEMs of sect. *Genea* species; magnifications are indicated by bars. Base of the 2nd floret (callus/scar area).

- 41. MA. Callus/scar: round/circular.
- 42. RU. Callus/scar: round/circular.
- 43.* FA (E mediterranean specimen). Callus/scar: circular/round.. Described by Scholz (1987) as semiorbicular/orbicular.
- 44.* FA (E mediterranean specimen). Callus/scar: round/obovoid, intermediate morphology between Figs 43 and 45 which is not referred to by Scholz (1987).
- 45.* FA (type specimen from Sicily, W mediterranean). Callus/scar: round/shortly elliptic. Described by Scholz (1987) as parabolic/ovate.
- 46.* FA (E mediterranean specimen). Callus/scar: round/elliptic. Extreme elliptic morphology which is not referred to by Scholz (1987).

*bar = 100 μ m.



area of mechanical breakage



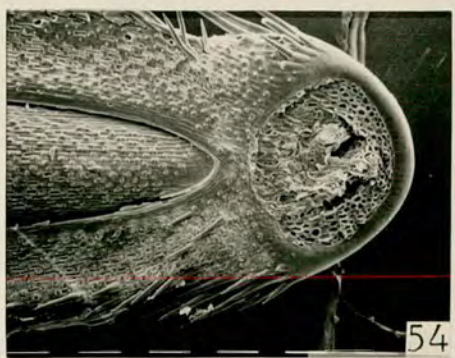
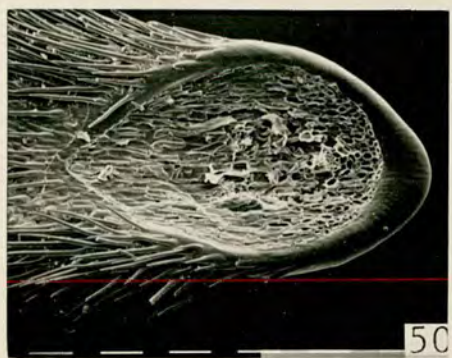
abscission layer
(callus area)

base of callus/scar (rounded fig.45;
pointed fig.47)



FIGURES 6.2.47 to 6.2.54. SEMs of sect. *Genea* species; magnifications are indicated by bars. Base of 2nd floret (callus/scar area) illustrating the continuous range of scar shape from elliptic to round and callus from pointed to rounded. Note the 3 vascular bundles visible in the centre of the scar, especially clear on Figs 51 and 54. Bar = 100 μ m.

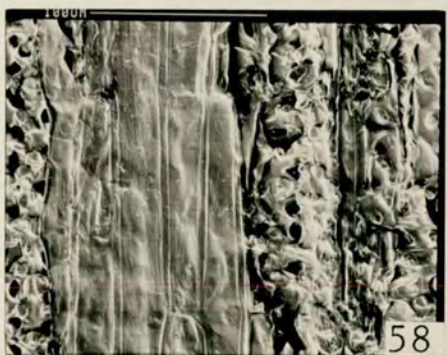
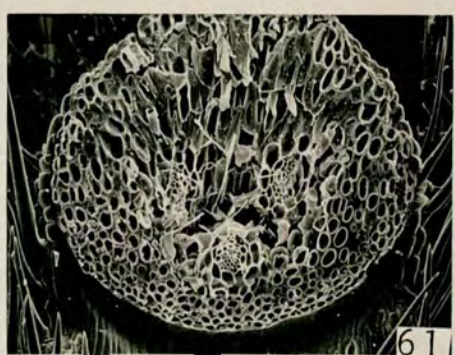
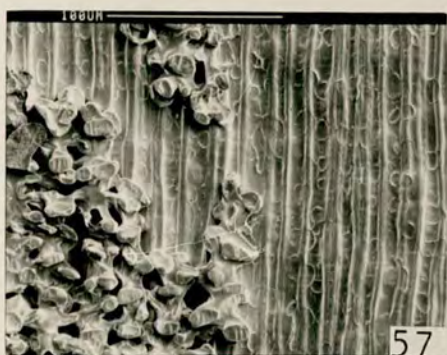
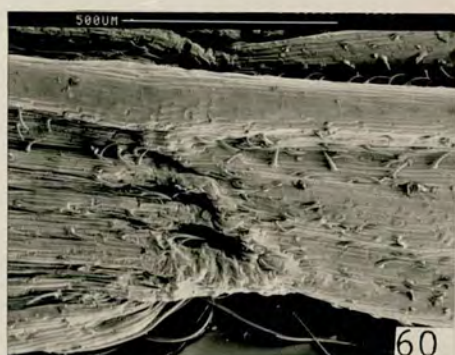
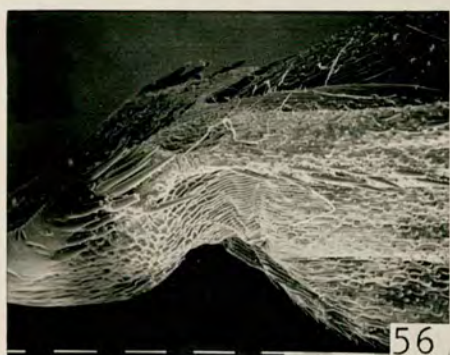
47. RI. Callus/scar: very pointed/elliptic. The combination of the long scar and long callus base with straight back of lemma (Fig. 55) partly account for the permanent imbrication of florets in a spikelet. The most contrasting situation is shown on Figs 54 and 56. Explanatory diagrams on Fig. 5.2.2.
48. RI. Callus/scar: very pointed/elliptic; intermediate morphology between Fig. 47 and Fig. 54.
49. DI/RI. Callus/scar: pointed/elliptic; intermediate morphology between Fig. 47 and Fig. 54.
50. DI/RI. Callus/scar: pointed/oval; intermediate morphology between Fig. 47 and Fig. 54.
51. DI. Callus/scar: pointed/oval; intermediate morphology between Fig. 47 and Fig. 54.
52. ST. Callus/scar: round/circular; intermediate morphology between Fig. 47 and Fig. 54.
53. ST. Callus/scar: round/circular; intermediate morphology between Fig. 47 and Fig. 54.
54. ST. Callus/scar: round/circular. The combination of the narrow scar and callus with articulation constriction at the back of lemma (Fig. 56) partly account for the spreading of florets in a spikelet. The most contrasting situation is shown on Figs 47 and 55. Explanatory diagrams on Fig. 5.2.2.



FIGURES 6.2.55 to 6.2.61. SEMs of sect. *Genea* species; magnifications are indicated by bars.

- *
55. RI. Base of 2nd floret: side view showing the absence of articulation constriction (contrast with Fig. 56). Explanatory diagram on Fig. 5.2.2.
- *
56. ST. Base of 2nd floret: side view showing the constriction that makes possible the spread out of the florets towards maturity (contrast with Fig. 55). Explanatory diagram on Fig. 5.2.2.
- 57. DI. Caryopsides surface showing the attached epidermal cells of lemma as a result of the glueing effect between the grain and the anthecium.
- 58. DI. Caryopsides surface showing damage of the outer pericarp, i.e. subepidermal, as a result of the glueing effect between the grain and the anthecium.
- 59. TE. Abaxial surface of leaf: auricle area showing a tissue differentiation that might be involved in the changing orientation of the blade.
- 60. RU. Abaxial surface of leaf: auricle area showing a tissue differentiation that can be involved in the articulation of the blade.
- *
61. DI. Top of 2nd rachilla segment: callus/scar area showing clearly the vascular bundles that will vascularize the 3rd floret. Whatever the division of the vascular bundles in a single floret, it seems that 3 always remain available for the next upper one.

* bar = 100µm



CHAPTER 7. CHEMICAL CHARACTERS (SEROLOGY)

7.1 INTRODUCTION

Plant systematic serology has encountered numerous difficulties over the past 100 years and only in the last 20-30 years has this approach gained the confidence of taxonomists. Early efforts are reviewed by Chester (1937), Moritz (1958) and Dahlgren (1983). Kloz *et al.* (1960) and Klozova & Kloz (1966) demonstrated that owing to their specificity, the antigenic components of plants represent valuable characteristics in taxonomic studies. Some of the pioneer work in modern plant systematic serology was carried out in *Bromus* by Smith (1969a; 1969b; 1976). The use of serology proved, indeed, to be most useful in suggesting or confirming relationships both at species level in *Bromus* and at generic level between *Bromus* and *Brachypodium*, *Triticum* and *Festuca*, but it was not used for taxa delimitation.

Recent work on the patterns of variation of proteins has shown that, at population level, isozyme differences occur within species (Derbyshire *et al.*, 1976) and that even at generic and higher levels of the hierarchy, some major seed storage proteins are highly conservative (Blüttner & Jensen, 1981). Serological methodology generally analyses 5-12 major proteins and probably shows no "interference" from the relatively minor differences which characterize different isozyme states - these being revealed by multiband acrylamide gel electrophoresis or electrofocusing. The basis of the serology rests upon variations of the fine surface shape (exterior antigenic determinants) rather than merely

the electrophoretic mobility of protein species. In this way serology can avoid confusions from minor variations of isozyme electrical charge and may indicate "surface phenomena" variations of highly conservative features, which may relate to packing efficiency and hydrolytic properties of storage proteins important in germination and establishment adaptations, related to niche.

Ideally, electrophoretic analysis with and without concomitant serological analysis, would be employed. In this study, exigencies of time and antiserum, together with a desire to expose primarily significant qualitative rather than quantitative differences, led to a concentration on carefully, replicated, double diffusion tests. It is hoped that circumstances will enable the extension of these tests in future.

Other macromolecular sequence based data, e.g. nuclear DNA hybridisation (Belford & Thompson, 1981), chloroplast DNA comparisons (Soreng, 1990), RFLP data, and automatic protein sequencing (Doolittle, 1981) offer alternative chemotaxonomic techniques (Smith, 1976; Harborne & Turner, 1984), but take time and resources not available in this study. These are all valuable guides to biochemical diversity, but have to be evaluated carefully in case their variation is not of the same order as the real biological discontinuities (i.e. "real" taxonomic, "real" biosystematic differences, Joysey, 1988). Some of them, at least, are more expensive in time and materials than immunological comparisons.

During the course of my own work on sect. *Genea*, I increasingly realised that its constituent species were very closely allied. It was, therefore, particularly interesting as I

came towards the end of my project, to see what information serology could give and whether or not it would agree with my own ideas on the inter-relationships of *Genea* species.

The base and principles of plant serotaxonomy are very simple, but the analysis and interpretation of the data can be, for a number of reasons, far more complicated. Extracts of proteins from particular taxa (antigens) are injected in animals inducing the formation of antibodies (within the antisera) in their blood. Some weeks later the antibodies are sampled from the blood. When this antiserum is tested against antigens from plants of the same and similar taxa, there is an antigen-antibody recognition interaction; an a-g/a-s complex forms and a precipitate is visible. The degree and nature of this precipitation is proportional to the degree of similarity between the extract used to raise the antiserum and the extract of the plant tested.

The tests can be made by simple double diffusion in which both the antiserum and the antigens diffuse towards each other, or else the antigens can firstly be electrophoresed to separate the proteins, and subsequently tested against the antiserum, again in a process of double diffusion (immunoelectrophoresis). Double diffusion resolves the reactions in terms of the size of molecules and how fast they diffuse. In immunoelectrophoresis the electrical separation of the proteins gives more information, e.g. more accurate estimate of the number of reacting complexes, but comparison between taxa are somewhat more difficult; on each plate only one antigen is run while in simple double diffusion many antigens are tested side by side against the same antisera.

The difficulties experienced by so many taxonomists, and by

myself, in analysing and interpreting this kind of evidence concerns not only the counting of precipitation bands but also the variability of serological resolution in different replicates. These technical difficulties can be overcome by greater accuracy in the technique and the production of many replicates. Simple a-s/a-g precipitation in liquid, followed by turbidometry (Fairbrothers & Petersen, 1983) gives a clear simpler result, but may obscure variation. However, whatever the method, there is an unavoidable factor to take into consideration: antiserum to different taxa have to be produced by different animals and each one has a different physiological reaction to them. Therefore, when reactions to these different antiserum are compared, the interpretation of the results has to be balanced and wise.

In the first approach I decided to sacrifice resolution to the possibility of a more accurate comparison. Therefore, for reasons given earlier, I used only simple double diffusion. Because immunoelectrophoresis is a more time consuming technique I have left it for a possible future stage (post-thesis) to confirm or test some of the double diffusion results. It has to be confessed that, due to the suspected very close relationship between the *Genea* species, no great differences in the protein patterns separated electrophoretically were in any case anticipated. A larger volume of antiserum will eventually be available on current plans.

Therefore, my serological results are not of such a scale that I could consider them as of major importance in themselves in formulating a classification, but certainly can give a valuable indication of the relationships of the taxa involved. This is

congruent with the generally post-delimitational use of immunological data by other workers.

In this work I tested, in simple double diffusion, the antisera of *B. diandrus* var. *rigidus* (RI), *B. madritensis* (MA₁), *B. sterilis* (ST) and *B. tectorum* (TE) against the antigens of *B. diandrus* var. *diandrus* (DI₁, DI₂), var. *rigidus* (RI), *B. fasciculatus* (FA), *B. madritensis* (MA₁, MA₂), *B. madritensis* var. *kunkelii* (MA_k), *B. rubens* (RU), *B. tectorum* subsp. *tectorum* (TE), subsp. *lucidus* (LU) and *B. secalinus* (the type species of sect. *Bromus* - BR). The TE antiserum was only feeble at the stage of test, so results with it are omitted here.

7.2 RESULTS

Some of the most interesting results are shown in Figures 7.1-7.4 and the analysis of the serological tests made is presented in Tables 7.1-7.3.

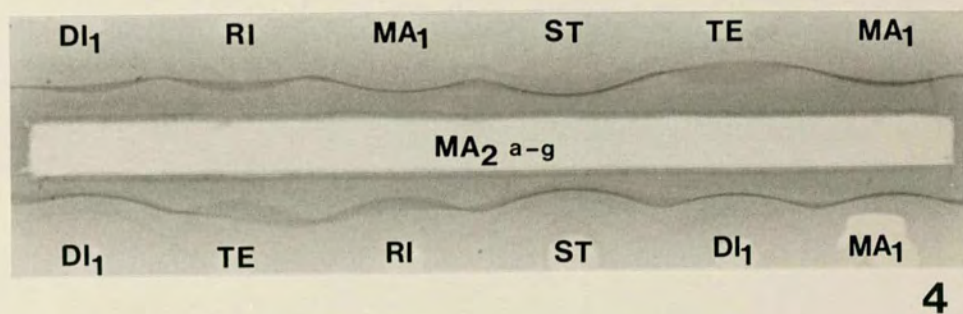
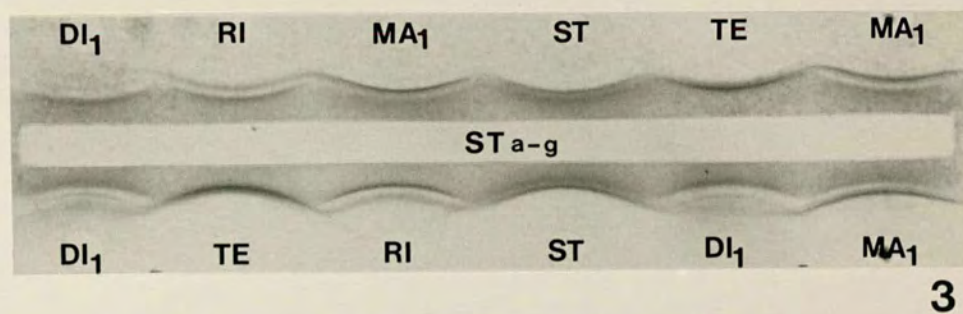
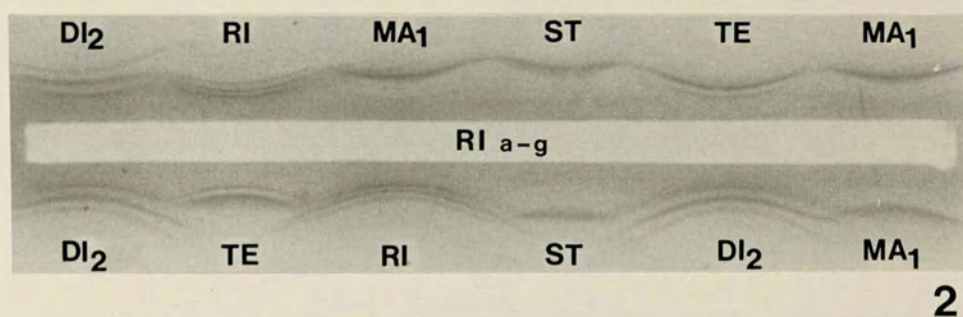
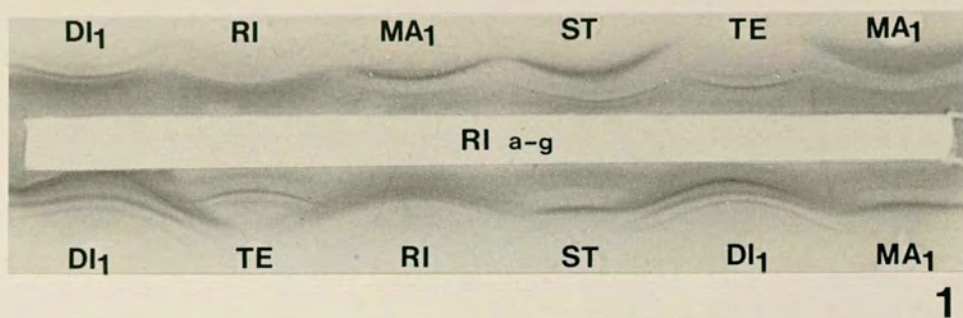
These notes cover only some of the results of the serological tests carried out. The technical inadequacy of some preparations and the absence of replicates were the reasons for not attempting a more comprehensive account. It has been decided to include here only data which can be presented, with some confidence, at this stage. Other wider testing has so far produced indications which are too "preliminary" to warrant inclusion.

7.3 DISCUSSION

The analysis of the serological results was made on the basis of the number of bands, the relative speed and strength of the overall reaction and the number of shared lines and spurs

FIGURES 7.1 to 7.4.

Double diffusion serological spectra of grain protein extracts of some sect. *Genea* taxa. Taxa are indicated by letters (cf. Chapter 2, Introduction, for meaning); a-g: anti-serum.



(apparent serological discontinuities) formed between adjacent antigens. The degree of precipitation (number of bands and the strength of the whole reaction) should be proportional to the degree of similarity between the antisera and antigen tested, as I refer to in the Introduction (7.1). Also the number of precipitation lines shared by adjacent antigens ("Common" or "shared" lines are those in a reaction which appear to fuse with lines in an adjacent reaction) indicates similarity between them. Similarly, the number of not-shared lines (indicated by the number of spurs) reveals serotaxonomic differences. Common, i.e. shared lines but mainly the number of spurs indicate the taxonomic relationship (distance) between the taxa tested.

The number of lines is most often 5-6 but they can be as few as 3 and as many as 8. Most of these lines represent common shared proteins (i.e. serological similarity) because the maximum number of spurs between two reactions is quite low, i.e. 1-3. Further, more than 50% of the reactions are quite strong and the speed of reaction of the different taxa was more or less the same. This general assessment of the serological behaviour of *Genea* species shows that there must be little differentiation between them, in these antigens, which confirms my other observations.

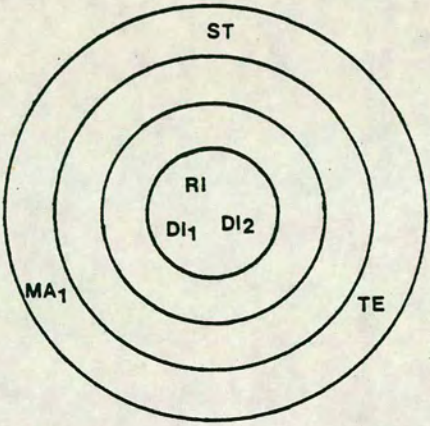
The relationships between species was evaluated mainly on the basis of the number of spurs formed between adjacent antigens.

(i) Results with RI-antiserum (Table 7.1)

DI₁ and DI₂ and RI gave identical serological reactions and ST, MA₁ and TE appear equally serologically distinct from RI. These data can be summarized on the following diagram:

TABLE 7.1. Serological (double-diffusion reactions) results using the antiserum to *B. diandrus* var. *rigidus*. Maximum numbers of non-identity (spur) reactions is indicated. The results are commented on.

RI a-s a-g	Total maximum no. of lines (approximately)	Strength of overall reaction	Spurring behaviour (spurs to)						Comments
			DI ₁	DI ₂	MA ₁	RI	ST	TE	
RI	8	strong	0	0	3	-	3	3	No difference recognized between DI ₁ and RI. DI ₁ , DI ₂ and RI are similarly distinct from MA, ST and TE
DI ₁	6	strong	-	-	3	0	3	3	No difference recognized between DI ₁ and DI ₂
DI ₂	6	strong	-	-	3	0	3	3	
TE	6	weak	0	0	0	0	0	-	This absence of spurring behaviour confirms the results above.
ST	6	weak	0	0	0	0	-	0	
MA ₁	6	weak	0	0	-	0	0	0	



(11) Results with ST-antiserum (Table 7.2)

The serological similarity of DI and RI, shown by RI antiserum, is confirmed both from the ST, MA₁ and TE "viewpoint". ST and MA are serologically very similar, but probably distinct because there seems to be a difference of serological distance between DI/RI and MA, on the one hand, and DI/RI and ST, on the other. The DI/RI-MA distance or difference seems marginally greater. TE is serologically further apart from the other taxa here involved. These data can be summarized in the following diagram:

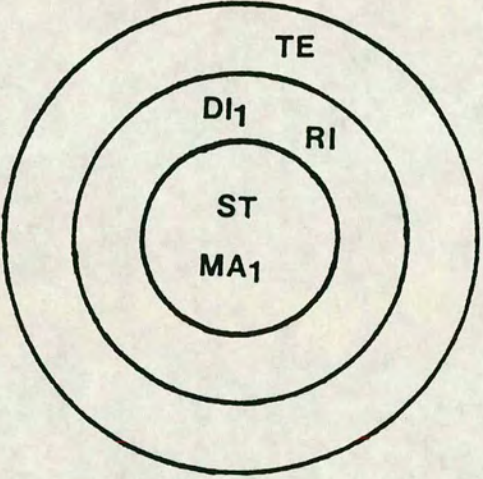


TABLE 7.2. Serological (double-diffusion reactions) using the antiserum to B. sterilis. Maximum numbers of non-identity (spur) reactions is indicated. The results are commented on.

* The absence of a spur is probably due to inadequate line resolving power of double-diffusion.

ST a-g a-s	Total maximum no. of lines (approximately)	Strength of overall reaction	Spurring behaviour (spurs to)						Comments
			DI ₁	DI ₂	MA ₁	RI	ST	TE	
ST	4(-5)	strong	1	-	0	1	-	0*	MA ₁ is serologically identical to ST. DI ₁ and RI are equally serologically distant from ST.
MA ₁	4(-5)	strong	2	-	-	2	-	2	MA ₁ is equally distant from TE, DI and RI.
TE	4	strong	2	-	-	2	0	-	TE is equally distant from both DI ₁ and RI.
RI	4	weak	0	-	0	-	-	0*	DI and RI are serologically identical
DI ₁	4	weak	-	-	0	0	-	1	

(iii) Results with MA₂-antisera (Table 7.3)

MA₁ antiserum shows finer distinction of the taxa involved than the ST and RI-antiserum.

The interpretation of the reactions where spurs did not form follows:

does not spur to:

MA₁ - DI₁, ST

MA₁, ST and DI₁ are very closely related.

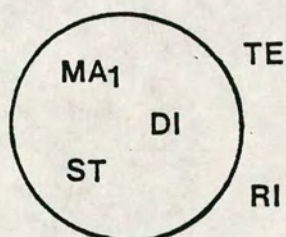
ST - DI₁, MA₁

RI - DI₁, MA₁, ST, TE

RI and TE differ more from MA₁ than the other taxa analysed in the plate.

TE - DI₁, MA₁, RI, ST

These data can be summarized in the following diagram:



The spurring behaviour of the taxa analysed is now commented on. The serological similarity, but not identity, of MA₁ and ST is confirmed; and the same can be said for DI₁ and RI.

All the information related to the reactions against MA₁-antisera are summarized in the diagram below:

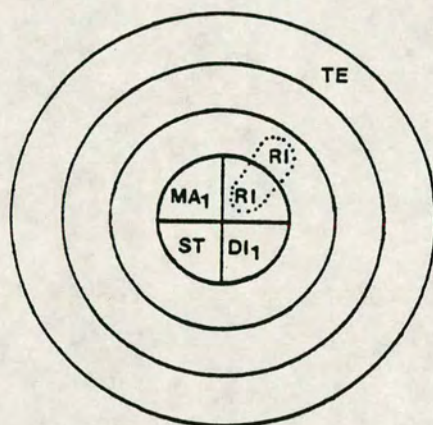


TABLE 7.3. Serological (double-diffusion reactions) results using the antiserum to *B. madritensis*. Maximum numbers of non-identity (spur) reactions is indicated. The results are commented on.

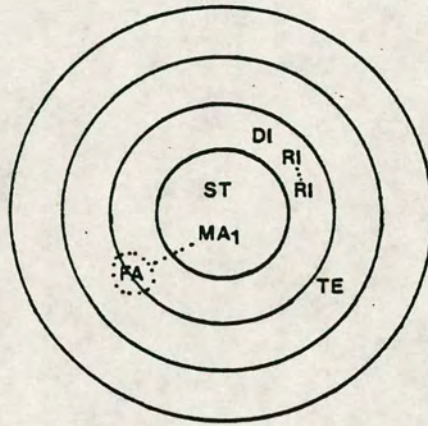
* These apparent anomalies are probably due to the inadequate line resolving power of double diffusion.

MA 2 a-s a-g	Total maximum no. of lines (approximately)	Strength of overall reaction	Spurring behaviour (spurs to)					Comments	
			DI ₁	DI ₂	MA ₁	RI	ST		TE
MA ₁	3*	strong	0	-	-	1*	0	3*	MA and ST are serologically distinct but never the less very similar
ST	4*	strong	0	-	0	2*		4*	ST is more serologically distant from RI and TE than from MA ₁
DI ₁	4*	strong	-	-	1	1*	1	2(-3)	D ₁ is closer to RI ₁ , MA and ST than to TE
RI	3	weak	0	-	0	-	0	0	Some differences recognized between DI and RI
TE	1(-2)	weak	0	-	0	0	0	-	TE and RI are more serologically distant from MA ₁ than DI and ST

7.4 CONCLUSIONS

Some of the data not presented here (which still require confirmation) seem to indicate that FA is distinct from the MA-RU group of taxa and that LU is serologically even more distinct from the core of *Genea* species than TE.

All the serological data presented can be combined in the following diagram:



On the basis of these serological data, with these antisera, ST and MA₁ seem to be at the core of the variation observed in sect. *Genea*. Two routes of differentiation seem to exist; one represented by the DI/RI group; another by a complex of taxa that comprises MA, RU, MA_k and FA. TE is serologically distinct from this central group of species.

Both the generally rather uniform and close serological response of the *Genea* species and the serological relationships do not contradict but rather confirm the indications of affinity obtained from other sources (anatomy, macro- and micro-morphology, strategies for dispersal biology and ecology), though the preliminary nature of these serological findings needs to be emphasised.

The natural follow-on from the basic serological approach in

Genea here presented (certainly meriting some further attention now that antisera are in production) will be the investigation of the cloudy area represented by MA, RU and FA. The apparently great serological similarities in this group of taxa requires a more precise analysis and therefore immunoelectrophoresis should be used. The links between sect. *Genea* and sect. *Bromus* via *B. tectorum* must also be investigated. It was unfortunate that the *B. tectorum* antiserum, of which much was hoped, proved to be only feebly reactive.

CHAPTER 8. CYTOLOGICAL CHARACTERS

8.1. INTRODUCTION

The first research on the chromosome numbers of the genus *Bromus* was published by Avdulov (1928). In this work, three species in sect. *Genea* were referred to: *B. madritensis*, *B. tectorum* and *B. villosus* (= *B. madritensis*). Stählin (1929), including a wider range of species, was the second author to work on this group. Since then, other researchers have worked on not only chromosome numbers (Table 8.1), but also their morphology (length, centromere position, number and position of active nucleolar organizers) and on some artificial hybrids.

In common with the majority of other genera in the subfamily Festucoideae, to which *Bromus* belongs, the basic chromosome number of *Bromus* is $n = 7$ (Avdulov, 1931; Darlington & Wylie, 1955; Löve & Löve, 1961), one of the basic chromosome numbers proposed for the family as a whole. Others numbers suggested are $n = 5$ and 6 (Flovik, 1938; Mehra *et al.*, 1968; Sharma, 1979; Stebbins, 1985).

Polyploidy occurs widely in *Bromus* (Table 8.2). In sects. *Genea*, *Bromus* and *Pnigma*, different levels of polyploidy have been recorded within the same species.

Aneuploidy is recorded in a few species of the genus. Apart from a reference to four extra chromosomes in *B. rubens* (Humphries, 1978) there is no other report of aneuploidy in sect. *Genea*. Allopolyploidy is reportedly common in perennials and autopolyploidy in annual species according to Kozuharov *et al.* (1981).

In *Bromus* sect. *Genea*, where the identification of the species is often so difficult, cytological observations have to be

Table 8.1 A chronologically arranged selective cytotaxonomic bibliography and guide to chromosome numbers of Bromus sect. Genea. In order to cut down on the number of references formally cited (under REFERENCES), I have not cited those in An.A.Fedorov, Chromosome Numbers of Flowering Plants (1969).
 GU - B. gussonei; MAX - B. maximus; MAC - B. macrantherus; RIN - B. rigens; VI - B. villosus. When authors consider Genea as the genus Anisantha it is referred to as A. on the table. For voucher specimens the herbarium code is given.

Reference		Information given by the authors				
Author(s)	Date	Species	Chr.No.	Country	Reference to techniques	Voucher specimens
Avdulov	1928	MA	2n=28			
		TE	2n=14			
		VI	2n=42			
Stählin	1929	MA	2n=42	Germany	Yes	None
		MAX	2n=56	"	"	"
		MAX var. gussonei	2n=28	"	"	"
		ST	2n=14	"	"	"
		TE	2n=14	"	"	"
Avdulov	1931	MA	2n=28	None	Incomplete	None
		ST	2n=14	"	"	"
		VI	2n=56	"	"	"
		TE	2n=14	"	"	"
Beck & Horton	1932	RU	2n=28	USA (California)	Yes	None
		VI	2n=56 70	"		
Tischler	1934	ST	2n=14	N Germany	Incomplete	None
			2n=14	"		
Sokolobskaya & Strelkoba	1939	LU	2n=14			
Cugnac & Simonet	1941	GU	2n=56	(possibly	Yes	None
		MA	2n=28	France)	"	"
		RI	2n=42	"	"	"
		ST	2n=14	"	"	"
		ST var. velutinus	2n=14	"	"	"
		TE	2n=14	"	"	"

Cugnac & Simonet	1941	OV	2n=56	No (poss-	Yes	None
		MA	2n=28	ibly	"	"
		MAC	2n=42	France)	"	"
		RI	2n=42	"	"	"
		ST	2n=14	"	"	"
		ST var. velutinus	2n=14	"	"	"
		TE	2n=14	"	"	"
Knowles	1944	MA	2n=28	USA (Cali-	Yes	None
		RI	2n=56	(fornia)	"	"
		RU	2n=28	"	"	"
		TE	2n=14	"	"	"
Schulz- Schaeffer	1956	RI	n=21	Non vidi	Non vidi	Non vidi
		RI subsp. MAX	n=28	"	"	"
		RIN	n=42	"	"	"
		RIN subsp. MAX	2n=56	"	"	"
		ST	2n=28	"	"	"
		TE	2n=14	"	"	"
Bowden	1960	TE	2n=14	Alaska	Yes	DAO
Bowden & Senn	1962	RI	2n=56	Chile	Yes	None
Sakamoto & Muramatsu	1963	MA	2n=14	Iran	None	None
Walters	1963	MA	2n=28	USA(Cali-	Yes	None
		RI	2n=56	fornia)	"	"
		RU	2n=28	"	"	"
		TE	2n=14	"	"	"
Gould	1968	DI	2n=56	USA(Texas)	Yes	UC,probably
Ovadiahu-Yavin	1969	FA var. alexandrinus	2n=14	Israel	Yes	HUJ
		FA var. fallax	2n=14	"	"	"
		MA var. ciliatus	2n=28	"	"	"
		MA var. glabriglumis	2n=28	"	"	"
		MA var. victorin	2n=28	"	"	"
		MA var. villiglumis	2n=28	"	"	"

		RI subsp.GU	2n=56	"	"	"
		RI subsp.RI	2n=56	"	"	"
		RU var.	2n=28	"	"	"
		glabriglumis				
		RU var.	2n=28	"	"	"
		rubens				
		ST	2n=28	"	"	"
		TE var.	2n=14	"	"	"
		hirsutus				
		TE var.	2n=14	"	"	"
		tectorum				
Fernandes & Queirós	1969	DI	2n=56	N & C of	Yes	None
		MA	2n=28	Portugal	"	"
		ST	2n=14	"	"	"
		TE	2n=14	"	"	"
Podlech & Dieterle	1969	TE	2n=14	Afghanistan	Yes	None
Gould	1970	RI	2n=28	Tunisia	None	US
		RU	2n=42	"	"	"
Dahlgren et al.	1971	MA	2n=28	Balearic	Yes	LD
		RI subsp.GU	2n=56	Islands	"	"
		RU	2n=28	"	"	"
Strid	1971	VI var. MA	2n=56	C Albania	Yes	LD
Queirós	1973	DI	2n=56	N & C	Yes	None
		MA	2n=28	Portugal	"	"
		ST	2n=14	"	"	"
		VI	2n=56	"	"	"
Kozuharov et al.	1974	MA	2n=28	Bulgaria	?	?
		ST	2n=14			
		TE	2n=14			
Loon	1974	MA	2n=28	Canary Islands	Yes	U
Chopanov & Yurtsev	1976	A.RU	2n=28	Turkmenia	Yes	None
		A.ST	2n=14	"	"	"
		A.TE	2n=14	"	"	"
		SE	2n=14	"	"	"
Humphries	1978	MA	n=14	Morocco	Yes	ZT
		RU	n=14	"	"	"
			2n=28+4B	"	"	"
		TE	n=7	"	"	"
			n=14	"	"	"

Natarajan	1978	RI	2n=56	France	None	MPU
Talavera	1978	DI	n=28	S Spain	Yes	SEV
		MA	n=14	"	"	"
Loon & Snelders	1979	MA	2n=14	Greece(Mt Olympus)	None	U
Natarajan	1979	RU	2n=28	S France	None	MPU
Sharma & Sharma	1979	TE	n=14	N India	Yes	PAN
Sokolovskaya & Prabatova	1979	A.DI	2n=56	Azerbaijan (Baku)	None	Probably
		A.RU	2n=28	Azerbaijan (Sumgait)	Yes(pollen)	LECB
		A.TE	2n=14	Armenia	None	
Esnault-Blanchard	1981	DI	2n=56	NW Africa	Yes	None
		MA	2n=28	"	"	"
		RI	2n=42	"	"	"
		ST	2n=14	"	"	"
Devesa & Romero	1981	ST	n=7	S Spain	None	SEV 50700
Strid & Franzen	1981	TE	2n=14	Greece(Mt Olympus)	None	C
Löve & Löve	1982	A.MA	2n=28	Italy (Toscana)	None	COLO

Table 8.2 The distribution and polyploidy level in Bromus and its sections. For sect. Genea the data are based on the bibliography presented on Table 4.6.1; some have been confirmed in the present work (Table 4.6.7). Data for other sections were based on Stebbins (1981) although by omitting to indicate the classification followed he makes it difficult to assess accurately some of his counts (e.g. species A, B and C in the table must be: A - B. arizonicus; B - B. erectus, B. inermis, B. macranthus and B. riparius. These species have other chromosome counts; C - B. erectus, B. macranthus. These species have other chromosome counts). The total number of species in each section is according to Smith (1970). Species with more than one level of polyploidy recorded were assigned a fractional value.

	Bromus sections							
Level of polyploidy	Annuals			Perennials				Total for Genus
	Boissiera	Neo- bromus	Nevskiella	Genea	Bromus	Cerato- chloa	Pnigma	
2x(2n=14)	1	0	1	3 ⁵ /6	9 ¹ /2	0	14 ¹ /2	30
4x(2n=28)	0	0	0	2	13 ¹ /2	0	11 ¹ /2	27
6x(2n=42)	0	1	0	1/2	0	7	7	15 ¹ /2
8x(2n=56)	0	0	0	1 ¹ /4	1 ¹ /2	7	5	14 ³ /4
10x(2n=70)	0	0	0	1/4	0	0	2(B)	2 ¹ /4
12x(2n=84)	0	0	0	0	0	1(A)	0	1
16x(2n=112)	0	0	0	0	0	0	1/2(C)	1/2
Total counted	1	1	1	8	24 ¹ /2	15	40 ¹ /2	91
Total species in sections	1	1	1	8	39	17	60	127

viewed with caution, even the published chromosome counts.

Apart from these uncertainties related to sect. *Genea* in particular, one has to bear in mind other factors that are relevant to all cytological studies when observing cytological material and establishing relationships among species based on chromosome morphology.

It is known that differences in chromosome size, with no difference in DNA content, occur between different tissues of the same plant and between cells at different stages of development of the same tissue (Dyer, 1979); therefore, most of the literature seems rather unreliable for any detailed conclusions about chromosome morphology. Furthermore, the different techniques used by the different researchers inevitably result in different degrees of contraction of the chromosomes making it difficult to compare the results of material from different provenances. In addition, it is most unlikely that metaphases recorded were at the same stage of chromosome contraction. In sect. *Genea*, most earlier publications lack clear information on the part of the plant and the treatment used, and very rarely is an analysis of the karyotype given (except for Kozuharov *et al.*, 1974 and Rychlewsky, 1970). For more reliable conclusions a standardized technique is essential: only the same kind of meristem is comparable and observations of a representative number of metaphases in one plant and in different plants are essential. However, where the literature covers a wide range of species, techniques and geographic distribution, conclusions can in general be accepted as reliable both for the genus and its sections.

With all the reservations mentioned above about records in

the literature, one can extract from it some general features of bromine chromosomes. The karyotype is quite symmetrical, both in relation to the complement as a whole and to each individual chromosome, the centromeres being median or submedian. My observations do not contradict these findings about morphology. It is difficult to determine what the evolutionary significance of the symmetry of a karyotype is (Dyer, 1979). Strong symmetry seems to show a low structural rearrangement of the chromosomes during evolution, while symmetry might have originated as a consequence of such rearrangement. However, the decrease and increase of symmetry might have followed each other during evolution. Therefore, it is sometimes difficult to indicate the evolutionary position of a karyotype. In the family *Poaceae* symmetric karyotypes occur so widely that trends towards asymmetry are likely to represent specializations.

Bromus chromosomes range from medium size to large, which conform to the size range of the other genera of subfam. *Festucoideae*. Stebbins (1981) points out that the general trend of evolution in *Bromus* has been towards an increase in chromosome absolute size. Therefore sects. *Genea* and *Phigma*, with the longer chromosomes should be the most evolved of all and the more primitive ones, the species in sects. *Neobromus* and *Ceratochloa*.

Earlier cytotaxonomic studies have much importance to satellite chromosomes and their morphology. Schulz-Shaeffer in 1960 identified no fewer than 15 morphological types of satellite chromosomes in *Bromus*. Assuming that the morphology of these chromosomes is constant, he proposed phylogenetic relationships among species. However, more recently Armstrong (1974) and

Stebbins (1981) were more cautious in this point and I definitely agree with their cautious approach. In fact, it is well known that the clarity of the morphology of these chromosomes can vary, not only in plants of the same population but even in cells of different organs of the same plant (Stebbins, 1971; Dyer, 1979; K. Jong, in litt.). Furthermore small duplications and deletions, that so often occur in the chromosomes, are enough to alter substantially the morphology of a satellite. It is unwise to assume relationships between species on the basis of this feature unless there are other supporting characters.

A preliminary study of the heterochromatin patterns in sect. *Genea* was referred to by Kozuharov *et al.* (1981). This study also includes several other annual and perennial brome grasses. Although heterochromatic segments are relatively inert in a genetic sense and in many cases the individual (animal or plant) can exist quite well without them, it seems that they have adaptive properties. The fact that Kozuharov *et al.* (1981) suggests that annual brome grasses have more heterochromatin than perennials might indicate a structural greater plasticity of annuals.

In *Bromus* sect. *Genea* apart from Rychlewsky (1970) who presented a careful study of the karyotype of a few species (*B. sterilis*, *B. tectorum* and *B. madritensis*) and Kozuharov *et al.* (1981) who offered an evolutionary interpretation of the heterochromatin pattern between annual and perennial bromes, all other cytological reports refer only to chromosome counts.

As already indicated, the species of sect. *Genea* are not always easy to identify and some of the published counts for particular species may well have been based on misidentifications.

B. rigidus can readily be confused with *B. diandrus*; *B. madritensis* with *B. rubens* and *B. fasciculatus*; and *B. tectorum* with *B. sericeus* (see Chapter 5). In addition to the difficulties that can be experienced with identification, the species present serious problems of cytological technique. It is frequently difficult to establish which is the best meristem to use and which is the best stage of development for treatment. And lastly, at least in the species studied in the course of this investigation, the chromosomes tend to clump together making counting difficult.

All these aspects had to be borne in mind when establishing a project of short duration into cytological studies on sect. *Genea*.

8.2 OBJECTIVES

Although only a short time could be allocated for cytological studies in sect. *Genea* [c. one month] it was thought to be useful if some work with restricted objectives was carried out.

Because of the problems of identification and difficulties with cytological techniques previously alluded to, I decided to concentrate on chromosome counts (making complementary herbarium specimens) and concomitantly to learn and improve the relevant techniques. A further objective was to make suggestions for further lines of cytotaxonomic research.

8.3 RESULTS

Table 8.3 lists the chromosome numbers counted by me and compares these with those from the literature. Illustrations of

Table 8.3 List of the mitotic chromosome numbers of root tips reported in B. sect. Genea. Provenance of material counted in the present work is referred to on Table 4.6.3 and previous records on Table 4.6.1.

Species	Chromosome numbers (2n) (my own counts)	Previous records	
		2n	n
<u>B. diandrus</u>	c.56	28/56	28
<u>B. fasciculatus</u>	14	14	-
<u>B. madritensis</u>	28	14/28/28+4B/42	14
<u>B. rigidus</u>	42	42/56/70	21/28
<u>B. rubens</u>	28	28	14
<u>B. sterilis</u>	14	14/28	7
<u>B. tectorum</u>	14	14	7/14

the chromosome complement of ^{some of} the species listed in Table 8.3 are in Fig. 8:1-3.

8.4 DISCUSSION AND CONCLUSIONS

My main contribution on the cytology of sect. *Genea* concerns the improvement of the technique used.

The most critical technical problems in the cytology of *B* sect. *Genea* are:

1) The number of divisions observed. This is always rather a low total whatever the conditions of germination, sampling of the material and the meristem used. Root tips apparently in the same conditions show some divisions or none at all. It seems that all parts of the plant have a long period of elongation and short periods of cell division; these are difficult to detect.

2) The chromosomes tend to clump together resulting in difficulties not only for the study of the chromosome morphology, but even in counting their number.

K.C. Armstrong (pers.comm., 1989) based on his experience with perennial brome-grasses kindly made some comments and suggestions on these technical problems, which I am glad to acknowledge.

Root Meristems

(a) Germination

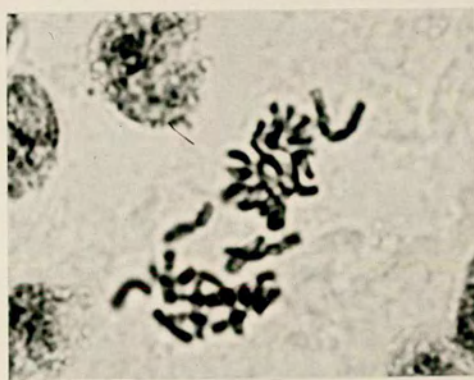
Condition no. 1 seems to be the one where a lesser number of divisions occur. Germination in dark either at room temperature ($\pm 24^{\circ}\text{C}$) (condition no. 2) or $+13^{\circ}\text{C}$ and dark followed by normal daylight and darkness at room temperature ($\pm 24^{\circ}\text{C}$) (condition no. 3) seemed to give similar results. However, I recommend

- Fig. 8.1 Karyotype of *B. tectorum*. Photograph of root-tip mitosis. The arrows indicate satellites. $2n = 14$.
- Fig. 8.2 Karyotype of *B. rubens*. Photograph of root-tip mitosis. $2n = 28$.
- Fig. 8.3 Karyotype of *B. rubens*. Interpretative drawing of Fig. 8.2. (Manton's method, 1950).



10 μm

1



10 μm

2



3

germination condition no. 3 as being the most similar to the natural conditions of germination of these plants.

(b) Sampling of the material

It seems there is no difference in the number of divisions observed in roots sampled by the three processes (α , β and γ). It was thought (Dyer, A., in litt.) that the emergence of secondary roots might reduce the number of divisions in the first one, but it is clear that this is not the case (at least in roots not longer than 2cm). Cutting the first root might have stimulated the formation of other roots but, in fact, it seems that this also is not the case.

The number of cells observed in division seems to be the same at 18.00 or 12.00, though somewhat higher in the morning. According to Armstrong (in litt.), in the perennial brome-grasses the best time to sample the material is 9-10 a.m. and 3-4 p.m. This needs to be investigated for *Genea* species because patterns of growth, cell division vs. extension growth and reaction to chemicals can vary quite a lot between different species even within the same genus.

Leaf Meristems

Leaf meristems seem to divide more intensively than root meristems. It is certainly an avenue to explore although the timing of sampling is more critical than it is in roots.

Ovaries and Anthers

Although there was not the opportunity to test much of the material collected or different species, it seems that, provided the ovaries and anthers are collected from very young florets, more divisions can be observed and the chromosome spread better

(even without pre-treatment) than in any other material observed. Because of the pale colour and small size, young ovaries and anthers are quite difficult to manipulate. Therefore, it is recommended not to dissect them but to cut and open the floret, to treat the material altogether and dissect the ovaries and anthers just before they are squashed. The ovary tissue in particular is soft enough to get good squashes without enzyme treatment.

The only inconvenient aspect of using ovaries and anthers in relation to growing material in petri dishes is that one has to wait a longer time for suitable material, i.e. for the plants to flower. Leaf meristems, ovaries and anthers produce clearer slides than the root tips. The root cap gives an opaque appearance to the slide and the greater thickness of the root tissue makes it more difficult to avoid cell overlapping.

Concerning the technique some comments are relevant. It is well known that Farmer's fluid produces a bubbly fixation of the chromosomes of some monocotyledons. This reaction was also observed with the present material. Of all the pre-treatments tested 1-bromonopthalene for 6 hours is by far the best one. Both 8-hydroxyquinolene and P-dichlorobenzene produced chromosomes always so clumped together that counts were impossible and its morphology extremely unclear. Armstrong (in litt.) observed the same effect of P-dichlorobenzene in perennial species.

The results with the cold pre-treatment (Table 4.6.3) were quite useless. Very few dividing cells could be observed and the chromosomes presented a distorted morphology. A relatively long

time of treatment was tested to try to accumulate as many divisions as possible but divisions could not be seen after 36 hours. Presumably, the metaphases complete their development in this time, perhaps more slowly, and the other cells stop dividing. Armstrong (in litt., 1989) mentions that for perennials 16-24h is the best time for cold pre-treatment and the ideal temperature +2°C; he also found that 0.1% colchicine 16-24 hours or even 48 hours is a good pre-treatment.

In my investigations the material tested without pre-treatment (control) gave just as good results as 1-bromonaphthalene. After this was established by a few replications the material was not submitted to any pre-treatment.

Both lacto-propionic orcein and acetic orcein stain methods induced many apparent distortions in the chromosome morphology and the cells have a not very clear cytoplasmic background. However, these two methods can be used for a quick assessment of the condition of the material. The red colour from Feulgen's reaction was visible after at least 45-60sec. becoming stronger with time. Because it is a selective stain it is very useful for localizing accurately the meristematic areas; something very important when using different meristems for the first time. Feulgen also seems to be the best stain for perennials (Armstrong, in litt.).

The chromosome numbers counted here confirm the most common ones recorded in the bibliography for every species except for *B. rigidus* (Table 8.4) where hexaploids and octoploids were previously encountered. The species for which several counts are cited in the literature are *B. diandrus*, *B. madritensis*, *B. rigidus*, *B. sterilis* and *B. tectorum*. As I have stressed above

Table 8.4 Chromosome numbers in B. sect. Genea species. Data collected from literature (Table 8.1 with 35 further references) and including my own results. Counts of B. "sericeus" are only recorded from the literature.

Species	No. of chromosome counts per species and per degree of ploidy					Total chromosome counts in a species
	14 (2n)	28 (4n)	42 (6n)	56 (8n)	70 (10n)	
<u>B. diandrus</u>	-	1	-	13	-	14
<u>B. fasciculatus</u>	3	-	-	-	-	3
<u>B. madritensis</u>	2	26	1	-	-	29
<u>B. rigidus</u>	-	-	12	16	1	29
<u>B. rubens</u>	-	19	-	-	-	19
<u>B. "sericeus"</u>	2	-	-	-	-	2
<u>B. sterilis</u>	18	-	-	-	-	18
<u>B. tectorum</u>	39	1	-	-	-	40

misidentification is a likely cause of these different counts. Such misidentifications are less likely to have occurred in *B. tectorum* ($2n=28$) as it is more readily distinguished from the other tetraploid species. Small *B. sterilis* plants can be confused with *B. madritensis*; and *B. madritensis* with a wide panicle can be confused with *B. sterilis*. Although there are big morphological differences between *B. madritensis* and *B. rigidus* they might have been confused in the past, both being diandrous, as Cugnac & Simonet (1941) state. For the same reason, *B. diandrus* could have been confused with *B. madritensis*.

More difficult to understand are the published chromosome counts of *B. rigidus*. The typical form of *B. rigidus* with its erect panicle and elliptic scar is easy to distinguish from *B. diandrus*, typically with a looser panicle and an oval scar. Intermediates are, in my opinion, more likely to be identified as *B. diandrus*, which is definitely octoploid. The similar number of records of both hexaploids and octoploids in *B. rigidus* may be the expression of either the real existence of two degrees of ploidy in this species or cytological indication of a complex of species involving *B. rigidus* and *B. diandrus* ($2n=56$). *B. rigidus* hexaploids have been recorded among introduced plants in America and among plants that grow in a large belt along the east and north of the Mediterranean and in the Atlantic side of the Iberian peninsula.

8.5 FURTHER LINES OF RESEARCH

The cytotaxonomic study of a group of species such as *B. sect. Genea*, where the problems of delimitation and identification

of species are so critical, is both stimulating and a challenge. The vegetative characters are fundamentally plastic and species identification relies mainly on reproductive ones. The basic consistency of the latter in plants of the same provenance growing in different conditions (see 4.2, phenotypic plasticity experiment) shows that at least part of their variation is genetically determined. The analysis of the cytogenetic base of this variation is very important in order to fully understand the evolution and relationships of these species. Therefore, three lines of future cytological work are clearly outlined as potentially profitable: the analysis of the karyotype; hybridisations; and analysis of chromosome behaviour at meiosis. It is hoped that this work, in general, will provide a sound future basis for the identification of the taxa being cytogenetically studied.

With all the reservations mentioned above, expanded studies of the karyotype (morphology of chromosomes in general and satellites in particular) and chromosome structure (patterns of heterochromatin) of all species can give important information either to distinguish/define species and/or to show how they can be related to each other. More chromosome counts, especially of *B. tectorum* subsp. *lucidus* and *B. fasciculatus*, from a wider range of populations are much needed.

Cugnac & Camus (1931) and Camus (1929, 1933, 1944) suggested the existence of some hybrids in sect. *Genea*:

- *B. x Husnoti* A. Camus (1929) = *B. madritensis* L. x. *B. maximus* Desf. [*B. rigidus*]

- *B. x fisheri* A. de Cugnac & A. Camus (1931) = *B. madritensis* L. x *B. sterilis* L.
- *B. Gussonii* Parl. [*B. diandrus*] = *B. sterilis* L. x *B. rigidus* Roth (1931)
- *B. Gussonii* var. *secundus* A. de Cugnac & A. Camus (1931) = *B. sterilis* L. x *B. B. rigidus* var. *gracilis* A. de Cugnac
- *B. x Rosettae* A. Camus (1931) = *B. madritensis* L. x *B. tectorum* L.
- *B. x granatensis* A. Camus (1933) = *B. madritensis* L. x *B. rubens*
- *B. x segoviensis* A. Camus (1933) = *B. rubens* L. x *B. tectorum* L.
- *B. Guetrotii* A. Camus (1944) = *B. sterilis* L. x *B. tectorum* L.

If these putative hybrids can be confirmed by artificial crosses, that can certainly help to clarify the relationships among species. Some other hybridizations are certainly very well worth trying. *B. sterilis* seems to me to have a quite central position as far as morphology is concerned, and possibly from an evolutionary standpoint as well, could be crossed with other species of the same section.

Although, as I refer to in Chapter 5.2, *B. diandrus* is not likely to be of hybrid origin (*B. rigidus* x *sterilis*) as proposed by Cugnac (1931) it would still be interesting to try this cross. The morphological variation of *B. diandrus* could then be the result of different degrees of genetic introgression between the two supposed parental species (*B. rigidus* and *B. sterilis*). A similar

situation is suggested to exist between, for example, *B. inermis* and *B. pumpellianus* (Armstrong, 1982).

B. tectorum constitutes a morphologically very distinctive group. Hybridisation of this species with other *Genea* species may help to clarify its evolutionary position. Artificial hybrids between typical subsp. *tectorum* and subsp. *lucidus* (*B. "sericeus"*) may well be extra evidence to support the subspecific rank that I proposed for *B. "sericeus"*.

Irregularities of chromosome pairing in meiosis in hybrids can lead to sterility of pollen grains. Pollen viability analysis can be, to some extent, quickly assessed using Alexandre's method (1969). Pollen grains from mature anthers are stained with cotton blue in lactophenol. Although non-functional pollen grains may stain with this dye, aborted pollen does not stain at all. This makes it possible to calculate, to some extent, the degree of sterility of a plant.

As far as material is concerned, it would be profitable to explore more deeply the potentialities of the leaf meristem and ovaries, studying the best timing for sampling the material. Developing ovaries, studied for their mitosis, seem on the basis of my work, to be the material of choice, in *Bromus*.

Certainly the most critical technical problem I dealt with was in obtaining good chromosome spreads. Testing pre-treatments with colchicine and cold at +2°C for different periods are according to my experience the most obvious further way to proceed.

CHAPTER 9. EVOLUTION AND ADAPTIVE RADIATION

9.1 INTRODUCTION

Even before the time of Socrates, such Greek natural-history philosophers as Anaximander (c.611-547 BC) and Empedocles (c.500-430 BC) had postulated bold theories of evolution in which man was regarded as merely another part of the natural environment.

However, with the decline of the Graeco-Roman world, the old Greek culture was almost dead and the anthropocentric philosophy developed during the Middle Ages opposed any concept of evolution. The humanist aspect of the Renaissance not only revived the Graeco-Roman philosophy, but also introduced the modern concept of science based on observation. As its ultimate aim is to understand humankind, biological science was most affected by the religious dogmas; and, as a result, not many major biological discoveries were made for a long time.

As late as 1748, the book *Telliamed* by Benoit de Maillet attempted to link cosmic and biological evolution in an all-embracing cosmology, reminiscent of the pre-Socratic Greeks. Although a man of vast knowledge, de Maillet was not really a scientist and his book, written in a popular fashion brought theories, heretical for the time, of cosmic and organic evolution, to many who would not have been reached by purely scientific works.

Buffon, Lamarck and Erasmus Darwin are some of the evolutionists who preceded Charles Darwin. But of them, Darwin (1809-1882) was the naturalist with most field experience and he offered the most plausible explanations of evolutionary processes: the theory of natural selection.

The huge diversity of living things suggested to Darwin different degrees of fitness in the struggle for survival; natural environmental pressures operated on all organisms selecting only those most fit to survive. Because only heritable variations are important in terms of evolution, these selected features are securely passed on to following generations. According to Darwin, natural selection leads to divergence of characters or speciation and, at the same time, to the extinction of less fit organisms and species.

As Darwin described it, the evolutionary process must be gradual and slow ["That natural selection will always act with extreme slowness; I fully admit ...". On the origin of species, p.108, 1859]. Nevertheless, he had confessed also that "... the periods during which species have been undergoing modification ... have probably been short in comparison with the periods during which these same species remained without undergoing any change" (*Op.cit.*) In spite of this "punctuation" hypothesis, by stressing the slowness of natural selection, the inadequacy of fossil records and the enormous length of geological time, Darwin left what can be called a "gradualistic" heritage.

The extreme punctualist explanations favoured by the geneticist De Vries (1905) and Goldschmidt (1940), in which evolution was supposed to be a dramatic transformation occurring by means of instantaneous genetic mutation, caused many biologists to turn more firmly to gradualistic principles. The publication of the famous Julian Huxley's Evolution: the modern synthesis in 1942 summarized the general acceptance of the gradualistic orientation given by Darwin in the previous century.

However, the accumulation of fossil records soon inspired Simpson (1944 & 1953) and Mayr (1954) to re-formulate general ideas on the pace of the evolutionary process. Since then, these ideas have been developed by evolutionists and paleontologists (Eldredge, 1971; Eldredge & Gould, 1972; Stanley, 1979). Nowadays, it is generally agreed that fossil species tend to exist over such long periods of geological time that, once formed, they must have evolved very slowly. When compared to the rapid pace of large-scale evolution this circumstance implies that the major evolutionary steps in the history of life must each have occurred in a very short period of geological time. This idea has been termed "the punctuational model" as opposed to the previous "gradualistic model" of evolution. These 2 models are depicted in Figure 9.1. The proliferation of new taxa in the punctuational model occurs rapidly by simultaneous divergence from not just one new kind of organism appearing, but many kinds diverging from a single ancestral group. Most of the evolutionary change occurs during this process that was called "adaptive radiation" by Simpson (1953, p.223).

It is necessary, however, to return to Darwin to find the reason for both the fast and slow processes of biological modification. The intimate relationships of organisms and their niche determines that any environmental change pressurizes individuals and induces the survival of the variations best adapted to the new environment. In my opinion "survival" is a better word than "selection". In fact, it is the "survival and expansion of the most able", not "selection by nature", that is the crux-factor in evolution. Combining mutation and

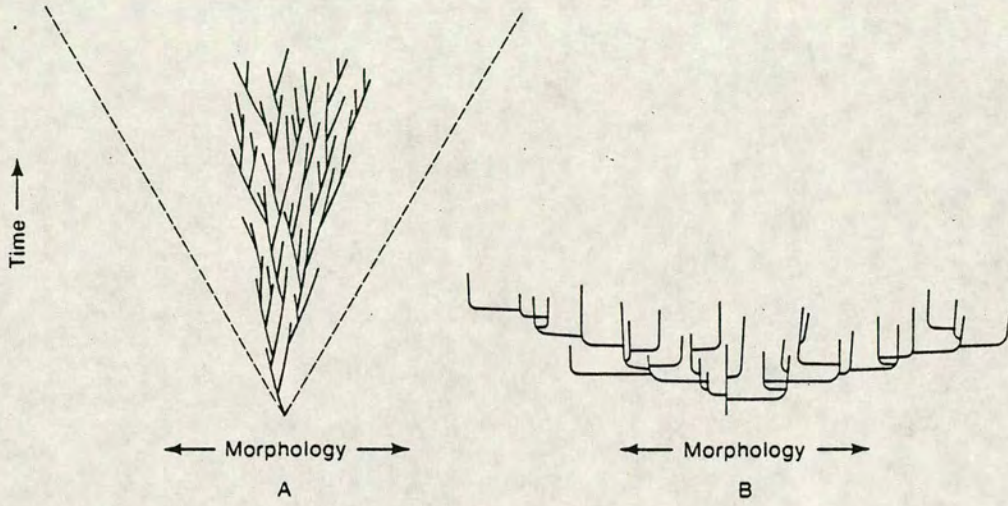


FIGURE 9.1
 Idealized phylogenies showing how, if phyletic evolution is slow, a strongly gradualistic pattern (A) permits much slower diversification than a strongly punctuational pattern (B). In the gradualistic model, rate of diversification cannot expand phylogeny beyond the area between the dashed lines, which represent the maximum rate of phyletic evolution.
 Reproduced from Stanley, S.M. (1979)

hybridisation, the net genetical potential for change is more or less uniform in many species (presupposing the same size of gene pool and inbreeding/outbreeding balance), and quite high, so that organisms are "prepared" for the process of speciation whenever niches change their character. In my view, it is more this potential that biologists were unaware of or not prepared to recognize, rather than that they failed to accept a fast evolutionary mechanism.

Evolution is quick when environmental transformation starts (climatic/geological/biotic-territorial invasion by animals or plants, new prospects for pollination or dispersal, etc. etc.) and it slows down as soon as organisms are reasonably well adapted to their new niches. The quick phase is thus the phase of adaptive radiation. Some continuous "final-tuning", involving minor and slower transformations, follows ("gradual period") during which optimal adaptations to a more or less but not absolutely stable niche occurs.

Because the process of adaptive radiation is very slow in terms of a human life-span and fossils are far from abundant, one of the best opportunities for biologists to study the mechanism of evolution is offered by organisms that are actually in the process of adaptive radiation.

As will be demonstrated later in this chapter, I believe *sect. Genea* is a fine example of such organisms and its study may bring a new insight to evolutionary processes in annual grasses.

9.2 EVOLUTION OF *BROMUS* IN EURASIA

It is generally agreed among agrostologists that the most primitive, now extinct, *Bromus* species probably differentiated in SW-C Asia during the Miocene, 25-11 My ago, (Stebbins, 1981). The evolution of this primitive stock seems to me to have occurred in 3 major steps:

- 1] the replacement of this primitive stock, now extinct, by more modern perennials;
- 2] the emergence of annual species;
- 3] the development of strong weedy tendencies in many of these annuals.

Again according to Stebbins (1981), the extinction of the primitive perennial stock and the formation of perennials similar to modern ones, now included in sects. *Ceratochloa* (New World) and *Pnigma* (Eurasia and New World), might have happened during the Pliocene (11-2 My ago). The dramatic physiographical changes that occurred by this time in the Mediterranean basin (Biju-Duval & Montadert, 1977) due to cyclical drying up of the sea were probably a pressurizing factor leading to speciation.

The shortening of the life cycle into an annual habit represented a major evolutionary trend which took place in many groups of flowering plants. In the same period of time, the number of generations is higher in annuals, i.e. sexual reproduction occurs more often. This encourages higher genetic diversification which, in turn, increases the potential for adaptation.

The massive formation of annuals in the genus probably occurred, during the Pleistocene, 2 My ago (Stebbins, 1981). By this time, the physiognomy of the landscape in the Mediterranean

and SW Asia had basically the same configuration as today, but major climatic pressures arose. The glaciations with the cyclical lowering of temperatures led to the formation of large extensions of ice that spread down from N Eurasia. Seventeen times, the ice extended variously southwards affecting N Europe, Alps, Pyrenees, Caucasus, Himalayas and the large inland seas in W and C Asia, narrowing the equatorial and temperate zones compared with today. These dramatic climate changes and the proliferation by this time of bovine ungulates in Eurasia, significant grazers of grass-lands, probably resulted in intensive grazing pressure, selection and rapid evolution (Scholz, 1975). The perennial species evolved into more complex species aggregates and their degree of ploidy increased. Eurasian species of sects. *Neobromus* and *Ceratochloa* might have become extinct. At this time, the more modern annuals probably evolved diversifying into what now are recognisably sects. *Bromus*, *Genea*, *Boissiera* (*B. pumilio*) and *Nevskiella* (*B. gracillimus*). It is likely that they occupied dry, open semi-arid habitats (Baker & Stebbins, 1945; Parsons, 1983). It is hard to indicate the time of origin of *Genea* but the current phase of adaptive radiation is probably related to one of the post-glacial ameliorations of climate.

The substantial differences_{in spikelet and floret shape} between sects. *Bromus* and *Genea* suggested to Stebbins (1981) a separate origin from different species of sect. *Pnigma*. The obvious morphological similarities of some *Genea* species with the *B. pectinatus* complex of sect. *Bromus* indicate, however, a stronger link with sect. *Bromus*. Figure 9.2 summarizes a speculative evolutionary process in the genus *Bromus*.

These new annuals were able to cope better with the seasonal

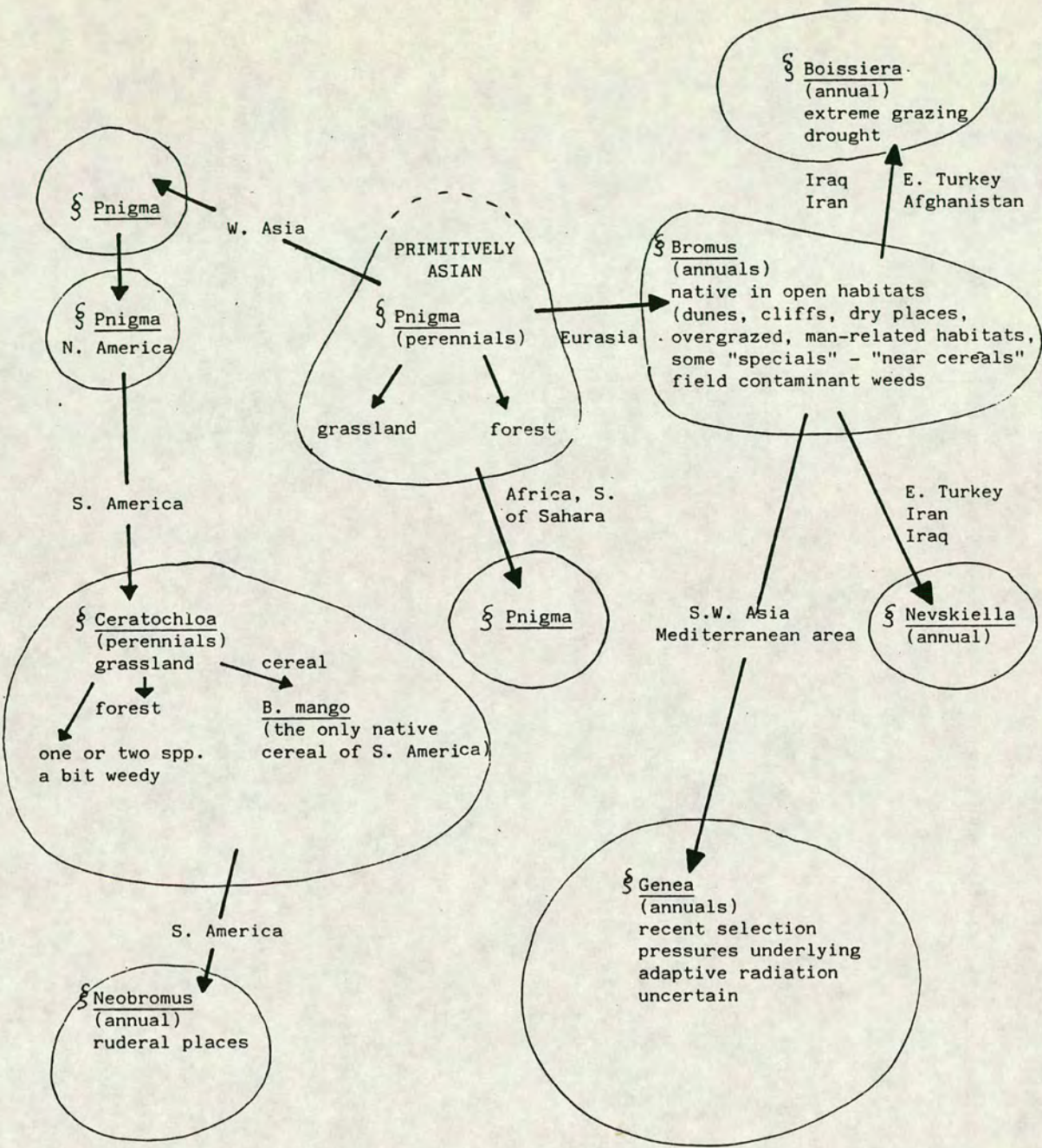


Fig. 9.2. ADAPTIVE RADIATION IN *BROMUS* IN RELATION TO SECTIONAL TAXONOMY
(compiled in association with P.M. Smith)

climatic regime in the warmer south of Europe and SW Asia. Here, the cool winters and dry summers "selected" those species able to complete their life-cycle within these 2 seasons. Many kinds of plants in these areas developed "weedy tendencies", which means ecological adaptations to "open", disturbed or unstable habitats with shallow soil and less competition from other plants (Hawkes, 1969). Probably these tendencies developed during the colonization of the new kind of habitat of bare, gravelly soil - left over by the extensive Pleistocene glaciers - insufficiently long-lasting to support a vegetation of a perennial nature. They also developed in the bare land left by grazing animals. These tendencies developed before the advent of man and he himself even further enlarged and multiplied such areas, providing many more opportunities for plants with weedy tendencies to spread and increase in numbers. The areas around his camps were rich in nitrogen and many of the weedy plants became especially adapted to fertilized soils.

The beginning of agriculture in SW Asia 9-10 thousand years ago brought not only the expansion of such ruderal areas, but also induced artificial selection. The ruderal behaviour of most of the annual bromes of sects. *Bromus* and *Genea* shows how, together with many other grass species, they must have exploited this pattern of ecological opportunity. There is also an indication that some species, especially in sect. *Bromus*, were affected by artificial selection during cultivation. The development of big grains and less efficient methods of dispersal (reduced or absent awns) is particularly clear in *B. secalinus* (Smith, 1973).

Although most species of sect. *Genea* are aggressive ruderals, it is not apparent that they were involved in this last

process of selection related to cultivation. Only *B. diandrus* has bigger grains and all species have rough, sometimes quite long awns. The evolutionary process of *Genea* although to some extent parallel to that of sect. *Bromus* seems to have followed a different process. Whatever this process is, it is not yet complete because the taxa involved are still not clearly differentiated. So it would be interesting to consider my taxonomic findings about *Genea* species in the context of the general evolution in the genus. That is, to analyse the biology of the situation suggested by my taxonomic conclusions. This is dealt with in the next section.

Finally, I would like to draw attention to some aspects of the timing of the evolutionary processes in *Bromus* just described. This is summarized in Table 9.1. The extraordinary diversification that occurred in *Bromus* over the last 2 My - c. 8% of the probable life span of the genus (according to the Stebbins theory, 1981) - is a fine example of the "punctuation phase" called adaptive radiation. In my view, the entire evolution of *Genea* species has occurred during this phase.

9.3 EVOLUTION AND ADAPTIVE ADAPTATION IN SECT. *GENEA*

The 8 taxa recognized in sect. *Genea* (Chapter 5) were associated by me in 3 species-groups:

1. *B. tectorum* subsp. *tectorum*
B. tectorum subsp. *lucidus*
2. *B. sterilis*
B. diandrus var. *diandrus*
B. diandrus var. *rigidus*

TABLE 9.1 Putative major events in the history of Bromus (modified after Stebbins, 1981).

Period	Epoch	Approximate time span (million years before the present)	History of <u>Bromus</u>
Tertiary	Miocene	25 - 11	Origin of archaic perennials species
	Pliocene	11 - 2	Differentiation of sects. <u>Ceratochloa</u> , <u>Phlisma</u> (perennials) and <u>Neobromus</u> (annuals)
Quaternary	Pleistocene (glaciations)	2 - 0.01	Differentiation of sects. <u>Bromus</u> , <u>Genea</u> , <u>Bolssiera</u> & <u>Nevskiella</u> ; development of the perennials with extinction of some species; development of strategies to deter grazing; emergence of weedy tendencies
	Holocene	0.01 - present	Development of weedy tendencies; artificial selection due to cultivation; annuals spread & diversify

3. *B. madritensis*
 (*B. haussknechtii*)
 B. rubens
 B. fasciculatus

These 3 species-groups have, I believe, some biological reality and the similarities amongst the species included in each share, in general, stronger relationships and closer evolutionary pathways than with species outside that group. However, in terms of affinities, *B. sterilis* could equally well be placed together with *B. madritensis* because it also shows links with it (see Chapter 5.2 and 5.3).

As normal in grasses (see Scholz, 1975; Stebbins, 1971; Clayton & Renvoize, 1986; Smith, 1991 in press) adaptations to habitat might be anticipated in inflorescence form, stem height, mechanisms of dispersal biology, leaf morphology and anatomy, awn shape, root system and callus/scar shape. I suggest also that in *Genea* the number of veins on glumes, a significant taxonomic character, must play an important role in the evolution of this group. It is not surprising that there is an obvious connection between these characters and the features exploited as characters by taxonomists. Good taxonomy expresses natural discontinuities of form and function.

An analysis of the characters referred to above, from the evolutionary view-point, now follows.

A. Inflorescence form

All species have erect and narrow, even switch-like panicles when young. This kind of morphology minimizes damage from wind and

abrasion with other plants and other biotic or physical features of the environment at a time when the reproductive structures are particularly fragile. However, in each of the 3 species-groups there are 1-2 taxa with long panicle branches. Early in the development of these plants, the panicles widen and the spikelets are individually exposed. In *B. tectorum*, *B. sterilis*, *B. diandrus* var. *diandrus* and part of *B. madritensis*, the panicles are loose, flaccid, large, open, effuse and more or less drooping.

In contrast, in each of the 3 species-groups there is at least 1 taxon where the panicles remain stiffly erect and are always compact and congested developing into tough and bristly structures. This is the case in *B. tectorum* subsp. *lucidus*, *B. diandrus* var. *rigidus*, *B. rubens* and *B. fasciculatus*. This kind of structure offers more protection to the florets enclosing them in a mass of lemmas, awns, glumes and branches and probably represents an adaptation to open, exposed areas where mechanical damage, transpirational water loss and grazing pressure are higher. In each of the 3 species-groups the taxa that have this kind of inflorescence are connected, within the group, with the driest areas or areas with uncertain or dramatically interrupted water supply, very high insulation and temperatures or, especially, a short growing season.

This kind of structure can be simpler, as in *B. tectorum* subsp. *lucidus*, than their looser-panicled counterparts and so, quicker to form and grow. It maximises the reproductive capacity (number of propagules) relative to the dry mass of the plant (raw material unit). Although the panicle of *B. fasciculatus* is of the same kind as *B. rubens*, it has in general fewer ramifications and

so is also simpler.

Plants with looser panicles have properties opposite to those listed above. They are to be expected, *a priori*, to grow in shadier, wetter, less exposed and stressed places; they, probably, are a more typical primitive form of grass panicle of more stable habitats of open woods and forest margins. Scholz (1975) and Smith (1991 in press) both consider loose panicles and wood-margin habitats to be primitive in such grass groups. Smith points out that "shaken" plant organs grow slowly. The switch-form of panicle so useful in the early stages (Smith, 1991 in press), becomes less-adaptive or non-adaptive at maturity when abrasion is necessary for dispersal.

Stebbins (1982) suggests that the multiplication of branches at a node is a secondary feature of the grass inflorescence and regards panicle structures such as that of *B. diandrus* var. *diandrus*, with solitary, paired or whorled primary branches, one of the basic forms of panicle morphology. On this basis the evolution of panicle structure in *Genea* could be as described in Figure 9.3. Solitary, paired and whorled primary branches, like the even simpler structure of *B. sterilis*, could have been the starting point for the increase of primary branching and the addition of secondary branches in *B. diandrus* var. *diandrus* and *B. madritensis*. A later shortening and multiplication of the branches in a *B. madritensis*-kind of structure could have been the origin of the very condensed panicles of *B. rubens* and *B. fasciculatus*. *B. diandrus* var. *rigidus* has basically the same kind of panicle structure as *B. diandrus* var. *diandrus*, but the branches are shorter. *B. tectorum* subsp. *lucidus* is simpler than *B. tectorum*

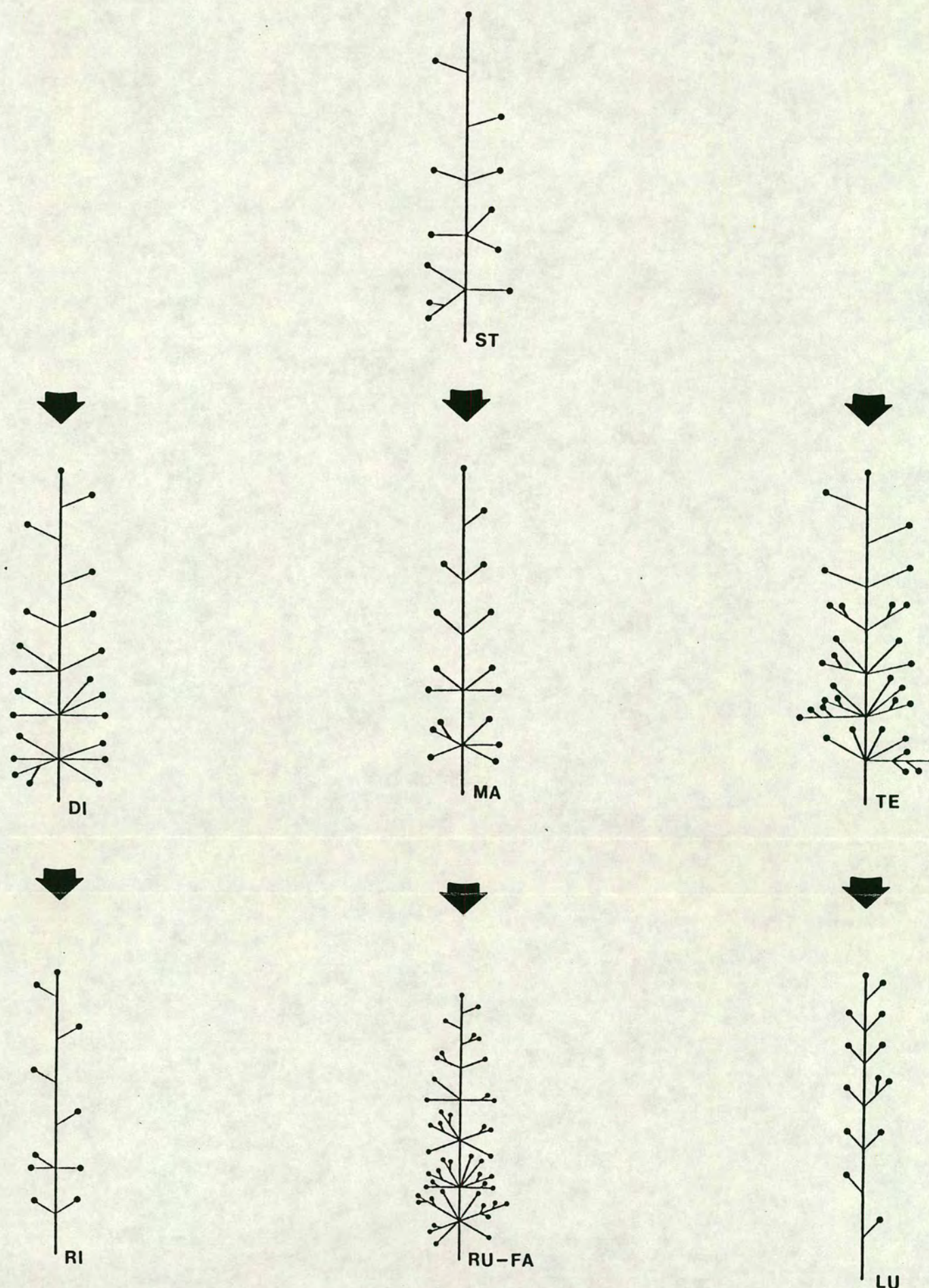


FIG. 9.3. Possible evolutionary trends of panicle morphology in sect. Genea. At the top is the putative primitive form with very few branches per node and very few or no secondary branches – probably growing in open woods and forest margins.

The 1st evolutionary tendency seems to have been an increase in the number of both branches per node and secondary branches, resulting in a higher number of propagules per plant. B. tectorum has the greatest increase in the number of spikelets and this might represent a compensation for the loss of propagules with the development of sterile florets related to dispersal biology. The 2nd evolutionary tendency relates to strategies to cope with the driest and hottest areas of the geographic/climatic range in Genea. Here, 2 opposite strategies developed: one towards simplification of panicle structure (B. rigidus & B. tectorum subsp. lucidus); the other towards a very considerable increase in complexity (B. rubens & B. fasciculatus). The panicle simplification with reduction in number of propagules might be related to the development of more precise devices for survival, such as pointed callus scar in B. diandrus var. rigidus that aids burial and synaptospermy in B. tectorum subsp. lucidus related to making the most of germination conditions. The dramatic increase in propagules per plant in B. rubens & B. fasciculatus might well be related to the wider range of strategies for survival that include short and long-distance dispersal. These issues are also discussed later in this chapter.

subsp. *tectorum* as discussed in some extent in Chapter 5.1, and I view it as a retrogression by reduction to a more basic form in a climate and a habitat where it is necessary to save energy, water and resist grazing.

Although panicle shape, as indeed are many other characters, is not totally differentiated among most of the *Genea* species, it is a useful indicator of evolutionary lines within the section that are, in many instances, confirmed by other characters as will be discussed later in this chapter. It is also most interesting that, supposed these theories to be accurate, fossil evidence being lacking, the loose kind of panicle of woodlands in each of the 3 species-groups must have been the core for 3 parallel evolutionary lines that produced condensed panicles adapted to dry, even to semi-deserts, in each group.

B. Dispersal biology, anchorage and establishment (ecesis)

Being annuals, it is extremely important for these plants to ensure, apart from some long-distance dispersal, the local continuation of the population in the next season. The balance or compromise achieved between these 2 opposite tendencies is mirrored by the spikelet structure and panicle shape and can be related to the kinds of pressures upon the plant. Also, the morphological devices developed often serve different modes of dispersal, e.g. exozoochory and anemochory, as referred to by Plitmann (1986).

The dispersal and establishment of propagules in *Genea* is connected with the development of sterile and modified distal florets in a spikelet. As pointed out by Stebbins (1982), this

feature has little or no value in detecting general trends in grasses because it appears independently many times, either in particular genera (e.g. *Pappophorum*) or within a genus (numerous examples exist in the *Aveneae* s.l.; also in *Melica*). However, I think that it can reveal major evolutionary tendencies at a lower level and certainly this is the case in *Genea* species.

In *Genea*, 3 major evolutionary lines concerning dispersal and establishment have emerged. Two of them seem to depart from *B. sterilis* in opposite directions; one, represented by the most distinctive forms of *B. diandrus* var. *rigidus*, favours local establishment; the other led, eventually, to the differentiation of *B. fasciculatus* and combines both long-distance and local dispersal strategems. A very different strategy seems to have determined major aspects of the differentiation of *B. tectorum* subsp. *lucidus* from *B. tectorum* subsp. *tectorum* and is discussed in some length in Chapter 5.1.6.

I shall consider first *B. sterilis* and the 2 lines that depart from it. The spikelets of *B. sterilis* disarticulate at maturity except for the uppermost 2-4 sterile florets that disperse together with the top fertile one. Although floret size is quite uniform, the top fertile one is smaller and the extra surface (wind-resistance) supplied by the attached sterile florets helps the whole set to be carried by the wind. This is the propagule that reaches longer distances - it has a 'sail'. The disarticulation of the spikelet is facilitated by the exposure of the florets towards maturity due, on one hand, to characteristic cuneiform development, achieved by the widening of the spikelet when each floret forms an angle with its base and the rachilla

segments curve; and, on the other hand, to the strategic positioning of the spikelets at the top of long branches in a loose, very open and mobile, panicle. The awns are long, straight and flexible without any obvious feature (apart from prickles) particularly useful either for dispersal or anchorage. The grains, of medium size within the section, are light enough to be carried by the wind, but probably not at great speed, thus covering relatively short distances. As I have mentioned for the panicle in particular, the whole reproductive structure in *B. sterilis* is the least specialized within the section.

The evolutionary line formed by *B. diandrus* var. *diandrus* and *B. diandrus* var. *rigidus* shows reduction of the exposure of the florets to the environment (discussed at great length in Chapter 5.2.3.3). This protection arising from panicle and spikelet congestion prevents, or reduces, cross-pollination, but also restricts dispersal. *B. diandrus* var. *diandrus* must represent the first or an early step in this still evolving line of adaptive radiation of which the most distinct forms of *B. diandrus* var. *rigidus* are, for the moment, the climax. Not surprisingly, the intermediate morphology of *B. diandrus* var. *diandrus* has been pointed out by several taxonomists. The opportunity for adaptation to drier and sandy places of a species, initially from the edges of open woodlands, would have required structural (and certainly some physiological) modifications. The most distinctive forms of *B. diandrus* var. *rigidus* have a contracted, quite simple, panicle adapted to exposed dry places and holds the grains tightly. The pointed, long callus/scar and non-articulation point, both at the floret base, together with straight rachilla segments are extra

features ensuring cohesion of the whole reproductive structure for quite a long time (for discussion at greater length see Chapter 5.2.3.3). The gain in grain weight prevents dispersal over great distances; the pointed callus favours rapid burying in sandy soils while the robust, erect rough awn keeps the grain lodged in its final position.

All these devices can be extremely important in windy places as is the case where this plant grows in coastal sand dunes. Several *Genea* species are ecologically catholic and adaptable: *B. diandrus* var. *rigidus* can grow also in other open places subjected to different kinds of pressures. Being introduced in the dry, extensive prairies of N America the species encountered a reasonable amount of dryness together with an alternative vector of dispersal - grazing herbivores, rare now in the places where the species grow in Eurasia, though Eurasian bisons and horses may have been a factor once. On one hand the continuous trampling ensures penetration of the pointed grains in the soil (local dispersal, maintenance of the population) sheltering them also during the frequent fires; on the other hand, the pointed grains and rough awns penetrate the wool (even flesh! - in the USA *B. rigidus* is called Ripgut Grass) and are transported over long distances by those animals (epizoochory). See also Thomasson (1985).

B. diandrus var. *rigidus* is probably the best example in *Genea* that illustrates the way adaptive radiation operates. In the centre of origin (Mediterranean region), the expansion of arid areas closed some niches and opened new ones to which a basically *B. diandrus* var. *diandrus*-kind of plant (*B. diandrus* var. *rigidus*)

only started to become adapted. It happens that this line of adaptive radiation is producing plants able to deal with very different kinds of pressures or react to opportunities which were not initially available. In N America, they were pre-adapted to overgrazed plains. The appearance of this third kind of environment surely started a new direction of adaptive radiation, diverging from the original one, and yet continuing at the same time.

In the other probable evolutionary line departing from *B. sterilis* and formed by *B. madritensis*, *B. rubens* and *B. fasciculatus*, the propagules seem to have developed some contradistinctive features to those of *B. diandrus* var. *diandrus* and *B. diandrus* var. *rigidus*, particularly adapted instead to long distance dispersal. The florets are smaller and diverge markedly from the rachis towards maturity. The grains are much lighter than in *B. sterilis* and often are \pm curved outwards. The awns also are outcurved. The sterile florets, that in *B. madritensis* are very similar to those in *B. sterilis*, evolved into a more complex structure of *B. rubens*, similar to the one developed in *B. tectorum* subsp. *lucidus* and described in Chapter 5.1.6. The number of sterile florets is higher in *B. rubens* (up to 7) and towards maturity they spread around the spikelet axis acting as a kind of parachute easily carried by the wind and taking with them only the top fertile floret. The curvature of the grain and awn is most highly developed in *B. fasciculatus* where the grain also twists almost 180° about its longer axis. The aerodynamics of the propagule are elaborated in *B. fasciculatus* (Fig. 9.4) and must be among the most effective for long distance dispersal in the whole

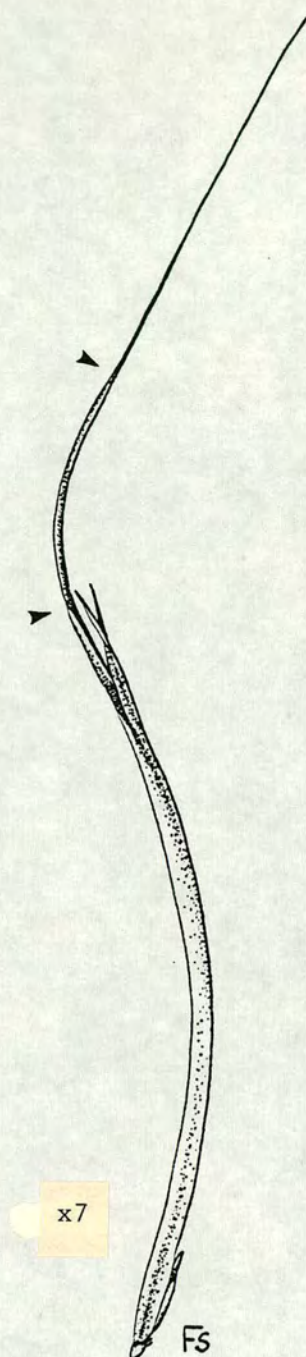


FIG. 9.4. B.fasciculatus: typical shape of propagule at maturity. The grain (and lemma) is outcurved and the awn is rotated upwards and twisted (▲), often twice as in this case. The whole set is delicate, light and aerodynamically very effective being easily carried by the wind(anemochory).

section, as simple tests demonstrate. The curved structures that trap the wind can themselves be trapped serving, then, the final purpose of anchorage.

But if the spikelets and their components seem to be particularly well-adapted to long-distance dispersal in this line of adaptive radiation the same cannot be said for the panicle structure. The shortening of the panicle branches in *B. madritensis* in relation to *B. sterilis* and the inexorably greater contraction in *B. rubens* and *B. fasciculatus* produced extremely compact panicles. These brush-like structures trap the propagules against themselves (this is clear even in herbarium specimens) using the features developed for dispersal and anchorage!

This combination of panicle, spikelet and floret structure seems to provide reasonable means for both local and long-distances to uncolonized, open places. All these features, in contrast to *B. sterilis*, imply open habitats (actually the kind of place these plants grow in), and anemochory must have been part of the opportunity for adaptive radiation in this small group.

The process of dispersal biology in *B. tectorum* subsp. *tectorum* and *B. tectorum* subsp. *lucidus* involving the adaptation of *B. tectorum* subsp. *lucidus* to semi-xeric conditions was already discussed in Chapter 5.1.6. The clear tendency towards an increase in the number of sterile florets and the development of synaptospermy are the main features of this group and unique in the whole section.

C. Stem height

As stressed previously (Chapter 5) this is a quite plastic character and in the discussion that follows variation of a plastic nature is not considered.

B. diandrus var. *diandrus* and *B. sterilis* are the tallest taxa in the section; *B. diandrus* var. *rigidus*, *B. rubens*, *B. tectorum* subsp. *lucidus* and *B. fasciculatus* much shorter. In each of the 3 species-groups, there is a taller and a much shorter taxon and the variation is parallel to the variation of habitat. The taller taxa are typically from more sheltered places; the shorter ones from open places, presumably because here the shorter plant is better protected from desiccation and grazing if closer to the ground. They achieve full height, at reproductive maturity, more quickly, so are at hazard from herbivores for a shorter time. All have considerable tillering ability following removal of the main stem: a feature of advantage in grazed, exposed areas. Of course, my presumed primitive habitat for these taxa - wood margins - is a grazed, exposed area. The height and habitat variation also correlate with the degree of panicle contraction. Contracted panicles on the top of short culms are better protected from the elements.

Because the typically taller taxa are adaptable enough to grow in nutrient-poor open places, it is difficult to assess the amount of variation due to plasticity or to genetic differentiation. The fact that most of these taxa are not yet clearly differentiated is an extra difficulty in identification.

D. Number of veins on glumes

Lemma and glume area may be a primary adaptative character related to photosynthetic area and/or dispersal biology (see Chapter 5.1.6); vein number may be a secondary, partly dependent, correlate to this.

Genea has been defined as having lower glumes 1-veined and upper glumes 3-veined. Although there is the exception of *B. tectorum* subsp. *lucidus*, with 3/5 veins, this general diagnosis was made to contrast especially with sect. *Bromus* that has more veins (3-5/5-7-9). However, I have observed that this vein reduction in *Genea* is only a tendency and is not totally differentiated. Occasionally, *B. sterilis* can have 3/5 veins, *B. diandrus* var. *diandrus* and *B. madritensis* can have upper glume 5-veined and the number of veins in *B. tectorum* subsp. *tectorum*, as discussed in Chapter 5.1.3.3, is very variable; in *B. tectorum* subsp. *lucidus* can even have 5/7 veins.

The number of veins on the glumes is, in fact, quite variable throughout the whole genus. The 2 perennial sections show opposite tendencies: *Ceratochloa* with 3-5/5-7 and *Pnigma* with 1-3/3-5. It is interesting that both high and low vein number is also present in the annuals. More veins in *Boissiera* (3-5/5-7) and *Bromus* (3-5/5-7-9); fewer veins in *Genea* (1-3/3-5-7), *Neobromus* (1/3-5) and *Nevskiella* (1/3). It is impossible to tell at this stage of knowledge of the whole genus how much these figures mirror evolutionary relationships or whether increase and decrease of the vein number happened at the same time in less related groups. Although I incline myself to the second alternative, I think that the number of veins on glumes may contribute to some

understanding of evolution at the lower levels of classification.

In 2 of the 3 species-groups considered in *Genea* (the one leading to *B. diandrus* var. *rigidus* the other to *B. fasciculatus*) there is a clear tendency for reduction related to the narrowing of glumes. In the third group (*B. tectorum* subsp. *tectorum* and *B. tectorum* subsp. *lucidus*), clearly related to *B. pectinatus* complex of sect. *Bromus*, the higher vein number is related to adaptation to semi-desert conditions (for detailed discussion see Chapter 5.1).

E. Leaf anatomy

Leaf anatomy is so intimately related to the basic biological processes occurring in plants that it can give important indications on physiological adaptations (Rahman, 1988). In the case of these grasses, the adaptations are related to dryness.

Rather than indicating any clear anatomical correlation with the evolutionary lines here discussed, the anatomical data given in Chapter 6 seem rather to show:

[1] Incomplete differentiation of the taxa in these characters. This is paralleled by the incomplete taxonomic distinction revealed by external morphology hence, pointing perhaps to their evolutionary youth.

[2] Several leaf features are likely to be involved in controlling temperature and water content in *Genea*. With some exceptions, the stomatal ratios (Table 6.1.2) show greater abaxial

stomatal ventilation in species from hotter, drier areas. With a perhaps anomalous value in *B. diandrus* var. *diandrus*, yet to be explained, the stomatal frequency per unit area is not very variable. Higher values in *B. tectorum* subsp. *tectorum* and *B. tectorum* subsp. *lucidus* perhaps indicate the greater need for leaf cooling via evapo-transpiration in hot climates.

[3] Some of the adaptations to dry places might not be of physiological, but rather of an ecological and/or "behavioural" nature. The shortening of a life-cycle is a way of evading water and temperature problems. In open ruderal localities in Portugal, I observed *B. diandrus* var. *diandrus* delaying its development at flowering stage due to an unexpected wet period with low temperatures in late spring. But as soon as temperatures and dryness increased the life-cycle was finished within 2 weeks. Also, in some cases (e.g. *B. fasciculatus*) the water supply may be greater than we recognize among the rocks and crannies where the plants grow. Although *B. fasciculatus* is in many respects similar to *B. rubens*, its physiological adaptations to dryness might be of a different nature from the one referred to by Killian (1942). The innumerable root hairs in *B. rubens* which trap and absorb water from condensation according to Killian, seem to be very reduced in *B. fasciculatus*.

F. Cytotaxonomy

Genetic data on *Genea* are sparse. The hybrids referred to in the literature (see Chapter 8) are only suggestions and not based on successful artificial crosses (e.g. *B. diandrus* var. *diandrus* =

B. sterilis x *B. diandrus* var. *rigidus*) and the identification of the parental taxa is doubtful due to lack of voucher material.

There is no detailed study of the chromosomes karyotype and it is unknown whether polyploidy arose by auto- or allopolyploidy. However, the complement has been established for all the taxa here recognized (Chapter 8). Four out of 8 taxa in *Genea* are diploid (*B. sterilis*, *B. fasciculatus*, *B. tectorum* subsp. *tectorum* and *B. tectorum* subsp. *lucidus*); two are tetraploid (*B. madritensis* and *B. rubens*); the other 2 are hexa- and octoploid (*B. diandrus* var. *diandrus* and *B. diandrus* var. *rigidus*). The increase in chromosome number must have occurred by quantum quantities (14 + 14; 28 + 14; 42 + 14). At the hexaploid stage ($2n = 42$), 2 taxa might have started separating. One *B. diandrus* var. *rigidus*, still with 42 chromosomes; the other, *B. diandrus* var. *diandrus*, continued the increase in chromosome number. As stressed before, they are not yet fully differentiated. Esnault-Blanchard (1981) pointed out that in N African populations only chromosome numbers can separate *B. diandrus* var. *rigidus* from *B. diandrus* var. *diandrus*. This, and of course the different chromosome counts for *B. diandrus* var. *diandrus* (see Table 8.3), mirrors, I believe, this on-going evolutionary process that, among other factors, involves polyploidy. The general low chromosome number of the section indicates recent origin.

If diploids are in some way implicated in the ancestry of the taxa of higher ploidy, then *B. sterilis* still is a good parental candidate for the origin of the 2 species-groups considered in *Genea* (i.e. the *B. diandrus* var. *rigidus* and the *B. fasciculatus* group).

H. Geographic distribution

Genea species are distributed in the Euro-siberian, Mediterranean, Irano-turanian and NE Saharo-sindian phytogeographical areas. If the areas of distribution of each taxon are simplified to the places where they are more common, one can say that *B. sterilis* is basically an Euro-siberian species; *B. tectorum* subsp. *tectorum* mainly Euro-siberian and Irano-turanian; *B. tectorum* subsp. *lucidus* is Irano-turanian with Saharo-sindian tendencies; and the others are mainly or exclusively (e.g. *B. fasciculatus*) Mediterranean taxa.

Of course, one has to bear in mind that most of them were introduced in many places. In some cases, there are records of their introduction, in other cases the plants are found only in obviously ruderal habitats (e.g. along coastlines, rivers, roads and railways; Wendelbo, 1956). This is especially true for *B. diandrus* var. *diandrus* and *B. madritensis* in N and C Europe. *B. sterilis* is becoming a segetal (weed in corn-fields) in northern Europe and I received letters from S England reporting *B. diandrus* var. *diandrus* as a noxious weed in cultivated ground. Introduction has been occurring over such a long period, since man was in the area, that often it is very difficult to decide whether a particular population is native or introduced (Smith, 1986). Exceptions are *B. fasciculatus* and *B. tectorum* subsp. *lucidus* that seem to grow only rarely in ruderal places and their geographical distributions (the smallest in the section) are probably the native ones. Although doing so well as a ruderal in N America, *B. diandrus* var. *rigidus* has also a quite restricted geographic distribution in the Old World, mainly around the Mediterranean

coastal area. The restricted distribution of *B. diandrus* var. *rigidus*, *B. fasciculatus* and *B. tectorum* subsp. *lucidus* agrees well with my opinion, expressed earlier, that in each of the 3 *Genea* species-groups these are the most recent taxa.

One can also speculate as to whether *Genea* species are invading or becoming extinct in the areas where they are less abundant. All the evidence gathered so far indicates that the original/primitive grass of sect. *Genea* was a plant with Euro-siberian characteristics. Once again *B. sterilis* seems to be the best candidate for this central position in the section, with its present main distribution in this area. In phytogeographical terms, it is clear that in each of the 3 species-groups there has been a progression into the more challenging niches made available by the contraction of the Euro-siberian kind of environment because of the desertification in areas where agriculture originated (Irano-turanian and Saharo-sindian areas) and also because of the expansion of the Sahara westwards. This is presumably the reason why nowadays most of the *Genea* species are less abundant in SW Asia than elsewhere.

In the suggested centre of origin of the section (Stebbins, 1981) only *B. tectorum* subsp. *tectorum* and *B. tectorum* subsp. *lucidus* are common. Their geographical distribution is interestingly parallel to other differences between this species-group and the other 2 groups in *Genea*. The unique geographical and morphological connections between *B. tectorum* subsp. *tectorum* and *B. tectorum* subsp. *lucidus* and the *B. pectinatus* complex (sect. *Bromus*), distributed more eastwards relative to *Genea*, might indicate that the section had a dual origin. A western phase in SW

Asia might have involved the origin of a *B. sterilis*-kind of plant; an eastern phase, linked to the *pectinatus* complex, may have generated *B. tectorum* subsp. *tectorum*.

What then might have been the parental taxa of sect. *Genea*? It is impossible to be precise, but the available data permit some generalizations.

The serological distancing of *B. tectorum* subsp. *tectorum* and *B. tectorum* subsp. *lucidus* from the other 2 species-groups is not big enough, in my opinion, to consider 2 totally distinct (although, of course, related) origins in the section and the 2 evolutionary lines departing from *B. sterilis* and *B. tectorum* subsp. *tectorum* must, in my view, have had a common ancestor (X), probably a very primitive species of sect. *Bromus*. I say very primitive because the species now regarded as highly evolved in the 2 sections seem to have followed 2, although parallel, well-differentiated evolutionary tendencies. Often in sect. *Bromus*, evolution seems to have occurred in connection with selection in agriculture. The grains are often big (e.g. *B. secalinus*, *grossus*, *bromoideus*, *arvensis* subsp. *segetalis*). The florets are shorter and broader, mimicking the cereal grains they infest. But awns remain as unspecialized as in the perennial grasses (straight terete, little photosynthetic tissue differentiated, etc.) and occasionally are even absent (e.g. *B. secalinus*) - that is, specialisation did not often involve dispersal, as is usually the case with plants domesticated as crops. In contrast to sect. *Bromus*, the most highly evolved *Genea* species seem to have opportunistic tendencies that made them the ideal colonizers of the arid spaces left behind by intense agriculture. This

"colonizing" ability is a consequence of its more specialized means of dispersal. The awns became more complex; their function in dispersal is often associated with the development of sterile florets; their photosynthetic function in the physiological adaptations to short life-cycles (probably active to the very end of the formation of the grain) might be crucial. The segetal behaviour of *B. sterilis*, comparable to some sect. *Bromus* species, might relate to its relative primitivity within *Genea* (e.g. bigger grains, less specialized means of dispersal).

Sect. *Bromus* did not seem to have the genetic potential to become a crop, though *B. secalinus* has occasionally been cultivated and this evolutionary option in the annual species of the genus seems now out of the question (*B. mango*, a grain of S America, no longer cultivated commercially, was a perennial of sect. *Cerathochloa*). Instead, the opportunistic evolutionary line of *Genea* and some less highly evolved species of sect. *Bromus* seems to be more successful just now. *Genea* may represent, therefore, one of the most recent, and probably one of the most extreme evolutionary events in the annual brome grasses within sects. *Bromus* and *Genea*.

The study of sect. *Bromus* is not in the scope of this thesis and my experience of it is very limited. For reasons of convenience, I initially considered *Genea* as a discrete group in the genus. However, I am now less convinced of that. One has to take into consideration the *B. pectinatus* complex (serologically very distinct from other sect. *Bromus* species, Smith, 1972) and those sect. *Bromus* species with more complex awns, also adapted to very arid places (e.g. *B. scoparius*). *Genea* is, in my opinion,

just a more specialized little group amongst a large evolving complex of annual brome grasses.

9.4 CONCLUSIONS

My own list of what can be considered primitive and advanced characters in *Genea* is given on Table 9.2. Some of these characters were discussed in evolutionary terms by Hubbard (1948), Stebbins (1982) and Davidse (1987) and agree with my own findings.

The process of adaptive radiation in *Genea*, as revealed by my results, is summarized in Figure 9.5. Although preliminary, my serological results support the relationships here described.

The centre of origin of *Genea*, according to Smith's criteria (1986) for annual brome-grasses (centre of genetic diversity; centre of greatest ecological range; centre of frequency; and presence of close relative) may be established as follows:

- SW Asia for the *B. tectorum/lucidus* group (SW Asia is their centre of genetic diversity; of greatest ecological range; centre of frequency and where most close relatives occur - the *B. pectinatus* complex);
- for the remaining species, although some of these criteria fail in SW Asia (i.e. it is neither their centre of greatest ecological range nor their centre of frequency), this is also probably their area of origin because their closest relatives grow there and it is the only area where all the species still grow (although some, e.g. *B. diandrus*, *rigidus* and *sterilis* are common only in the western areas).

This probable area is indicated in Figure 9.6. This centre of origin was affected during the various glaciations and so were the

TABLE 9.2 Primitive (listed first) and advanced state of characters in relation to sect. *Genea* species.

Habit:	perennial-annual
Life-cycle duration:	long-short
Height:	tall-short
Panicle:	open panicle-condensed
Panicle branches:	long-short single-ramified
Disarticulation of florets:	chorispermy-synaptospermy
Diaspore:	individual florets-1 fertile floret and sterile florets-individual spikelet
Florets:	all alike-differentiated few sterile - many sterile
Rachilla segments:	straight-curved
Lemma texture:	more like leaves (herbaceous)-less like leaves (e.g. less green tissue, hyalin margin) similar in texture-dimorphic
Callus:	undifferentiated, rounded-differentiated, sharp, pointed
Elongate callus hairs:	absent-present
Awn type:	straight-curved flexible-rigid not twisted-twisted terete-not terete single-trifid
Awn position:	terminal-dorsal
Stamens:	3-2
Caryopsis:	straight-curved flat-inrolled
Chromosome no.:	diploid - polyploid

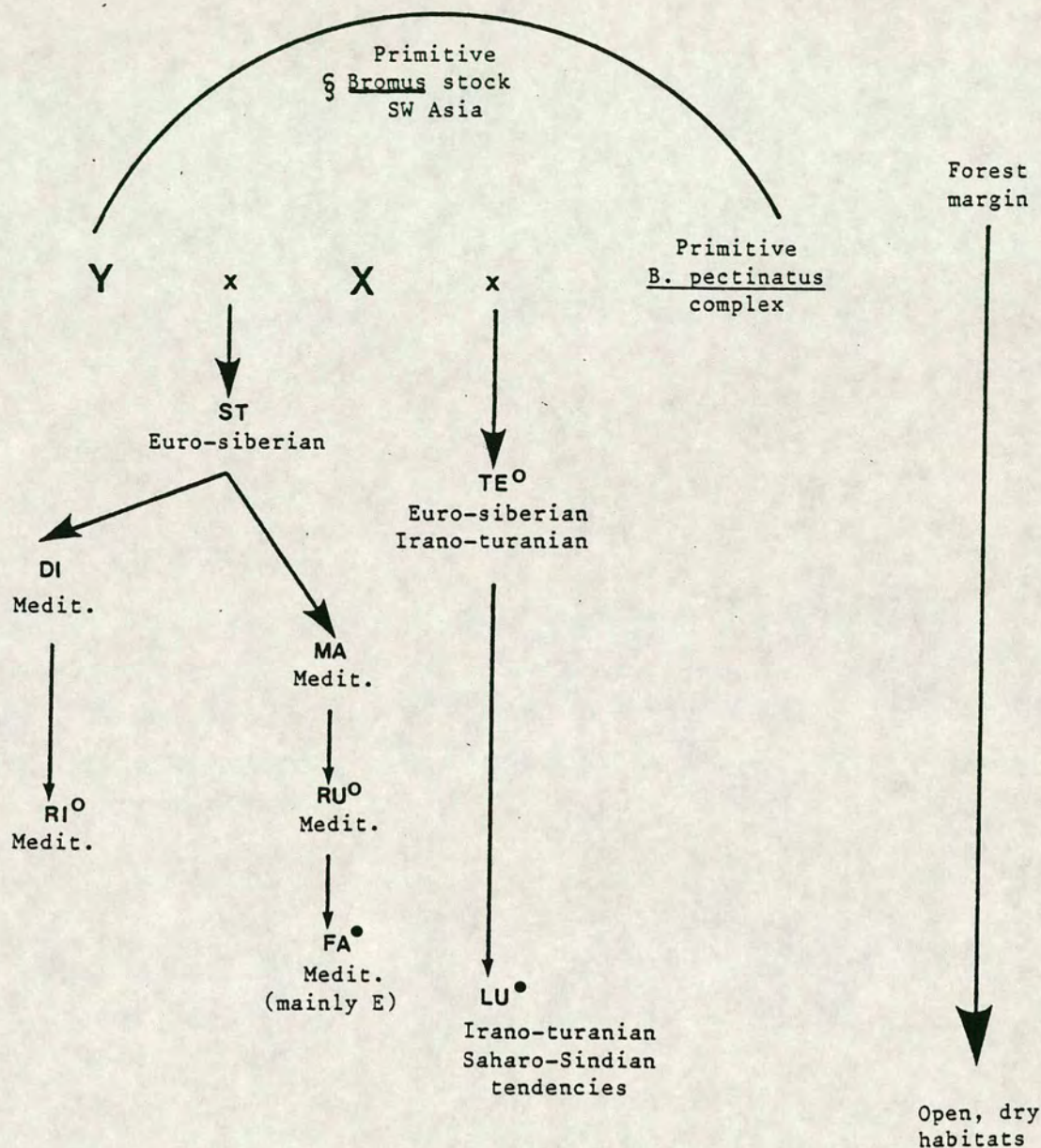



FIG. 9.5. Possible patterns of adaptive radiation in sect. *Genea*.


o taxa that constitute major introductions elsewhere - mainly N America


• taxa apparently growing in non-ruderal places.


The *B. sterilis* and *B. tectorum* evolutionary lines might have had a common ancestor - 'X'. 'Y' is then the other ancestor of *B. sterilis*.


FIG. 9.6 Sect. Genea in Eurasia.

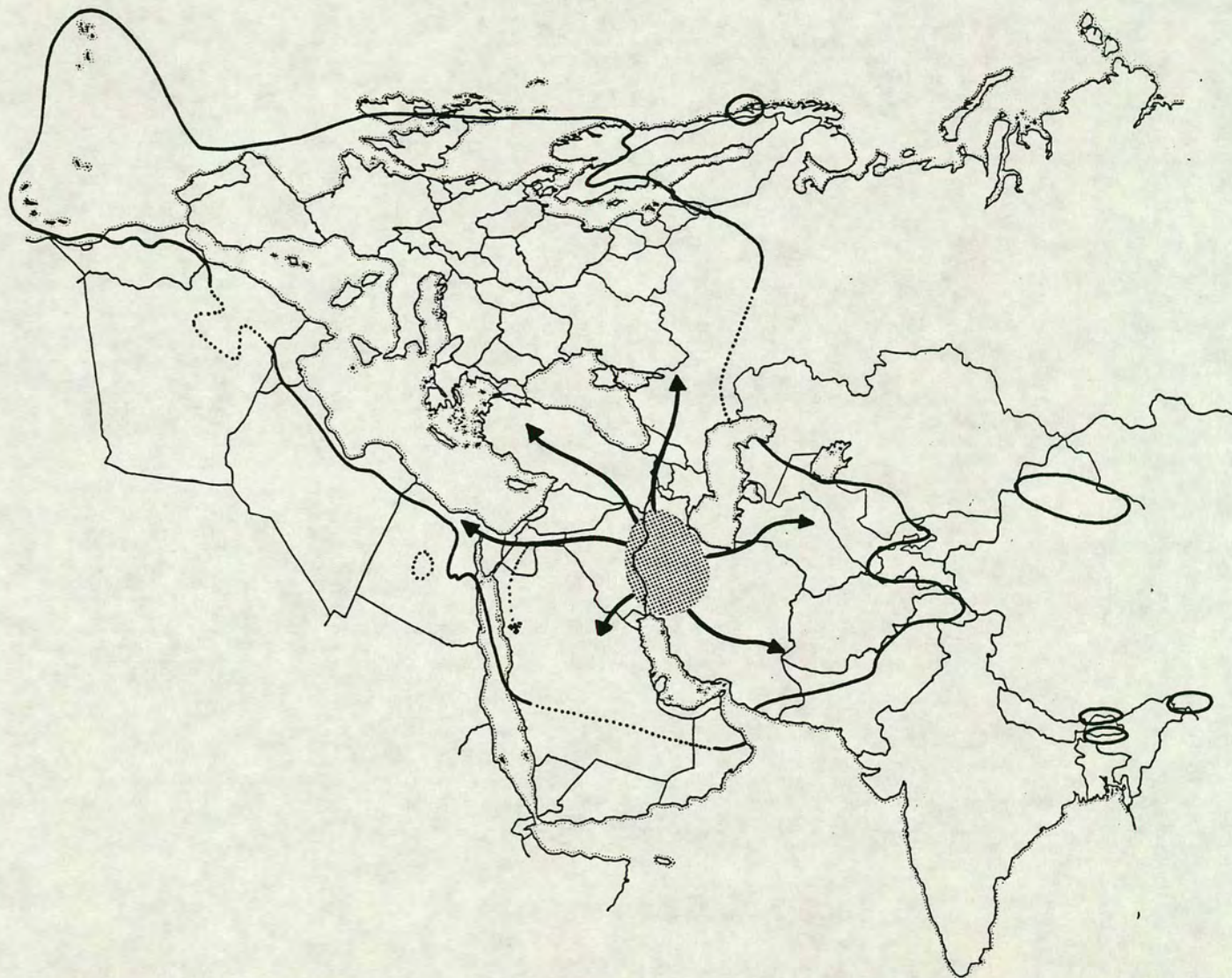
-  - Actual distribution of Genea species in Eurasia.

-  - Uncertain delimitation.

-  - Putative centre of origin of Genea species. According to Smith's (1986) and Webb's (1985) criteria to determine native status of a plant; this area was obtained by overlapping the presumed native distribution of each taxon and corresponds to the area common to the major number of taxa. This area is situated in SW Asia and this agrees with Stebbins (1981).

-  - Migrational trends in sect. Genea.

-  - Putative migrational route of B. fasciculatus in the Arabian peninsula.



taxa that spread from it during the inter-glacial periods. The net movement or radiation from the centre of origin occurred mainly westwards as indicated on Fig. 9.6 (Smith, 1986). It is possible that a secondary centre of origin for *B. tectorum* subsp. *lucidus* is emerging in the West in NW Africa, Canary Islands and SW of Iberian peninsula (see Chapter 5.1.3.4).

The link or association of "one species:one niche" is the basis of evolution. The recent emergence of a multiplicity of niches is probably the reason for the rapid simultaneous divergence of many new kinds of plants in *Genea* (adaptive radiation). The taxonomy here presented is, (as it should be!) only a description or statement of the present stage of a continuing evolutionary process.

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11. APPENDICES

APPENDIX 3.1

An alphabetical and chronological list of the species and infra-specific taxa of sect *Genea*, together with places of publication. Taxa described within the last 20 years are listed after No. 242.

NO	NAMES	PLACE OF PUBLICATION
1	<i>Anisantha diandra</i> (Roth) Tutin	<i>Fl.Br.Isles</i> , ed.2:1149 (1962)
2	<i>Anisantha fasciculata</i> (Presl) Nevski	<i>Act.Univ.Asia Med.</i> VIII b. Bot.17:21 (1934)
3	<i>Anisantha gussonii</i> (Parl.) Nevski	<i>Act.Univ.Asia Med.</i> VIII b. Bot.17:20 (1934)
4	<i>Anisantha madritensis</i> (L.) Nevski	<i>Act.Univ.Asia Med.</i> VIII b. Bot.17:21 (1934)
5	<i>Anisantha madritensis</i> C. Koch var. <i>ciliata</i> (Guss.) Tzvel.	<i>Fl.Europ.Chashi</i> SSSR 1:185 (1974)
6	<i>Anisantha pontica</i> C. Koch	<i>Linnaea</i> 21:394 (1848)
7	<i>Anisantha rigens</i> (L.) Nevski	<i>Act.Univ.Asia Med.</i> VIII b. Bot.17:20 (1934)
8	<i>Anisantha rigida</i> (Roth) Hyl.	<i>Uppsala Univ.Arsskr.</i> 7:32 (1945)
9	<i>Anisantha rubens</i> (L.) Nevski	<i>Act.Univ.Asia Med.</i> VIII b. Bot.17:19 (1934)
10	<i>Anisantha sericea</i> (Drob.) Nevski	<i>Act.Univ.Asia Med.</i> VIII b. Bot.17:20 (1934)
11	<i>Anisantha sterilis</i> (L.) Nevski	<i>Act.Univ.Asia Med.</i> VIII b. Bot.17:20 (1934)
12	<i>Anisantha tectorum</i> (L.) Nevski	<i>Act.Univ.Asia Med.</i> VIII b. Bot.17:20 (1934)
13	<i>Bromus abortiflorus</i> St. Amans	<i>Fl.Agen.</i> 44 (1821)
14	<i>B. ambigens</i> Jord.	<i>Billot, Annot.Fl.France & Allem.</i> 229 (1855)
15	<i>B. amplus</i> C. Koch.	<i>Linnaea</i> 21:418 (1848)
16	<i>B. asperipes</i> Jord.	<i>Billot, Annot.Fl.France & Allem.</i> 229 (1855)

NO	NAMES	PLACE OF PUBLICATION
17	<i>B. avenaceus</i> Pourr.	<i>Act.Toulouse</i> 3:308 (1783)
18	<i>B. boraei</i> Jord.	<i>Billot, Annot.Fl.France & Allem.</i> 230 (1855)
19	<i>B. canescens</i> Viv.	<i>Fl.Libycae Spec.</i> 5 (1824)
20	<i>B. ciliatus</i> Huds.	<i>Fl. Angl., ed.</i> 1:40 (1762)
21	<i>B. diandrus</i> Roth	<i>Bot.Abh.</i> 44 (1787)
22	<i>B. diandrus</i> Curtis	<i>Fl.Lond.</i> 6:t.5 (1828)
23	<i>B. diandrus</i> Roth f. <i>asperipes</i> (Jord.) Soó	<i>Acta Bot.Acad.Sci.Hung.,</i> 17(1-2): 115 (1972)
24	<i>B. diandrus</i> Roth f. <i>borai</i> (Jord.) Soó	<i>Acta Bot.Acad.Sci.Hung.,</i> 17(1-2): 115 (1972)
25	<i>B. diandrus</i> Roth f. <i>glaber</i> (Willk.) Soó	<i>Acta Bot.Acad.Sci.Hung.,</i> 17(1-2): 115 (1972)
26	<i>B. diandrus</i> Roth subsp. <i>maximus</i> (Desf.) Soó	<i>Acta Bot.Acad.Sci.Hung.,</i> 17(1-2): 115 (1972)
27	<i>B. diandrus</i> Roth f. <i>pilosus</i> (Dietr.) Soó	<i>Acta Bot.Acad.Sci.Hung.,</i> 17(1-2): 115 (1972)
28	<i>B. diandrus</i> Roth f. <i>propendens</i> (Jord.) Soó	<i>Acta Bot.Acad.Sci.Hung.,</i> 17(1-2): 115 (1972)
29	<i>B. dilatatus</i> Lam.	<i>Enc.I.:</i> 463 (1783)
30	<i>B. fasciculari</i> Ten.	<i>Fl.Nap.</i> V:17 (1830)
31	<i>B. fasciculatus</i> C. Presl	<i>Cyper.Gram.Sic.</i> 39 (1820)
32	<i>B. fasciculatus</i> C. Presl var. <i>alexandrinus</i> Thell.	<i>Repert.Sp.Nov.Fedde</i> 5:161 (1908)
33	<i>B. fasciculatus</i> C. Presl subsp. <i>delilei</i> (Boiss.) H. Scholz	<i>Willdenowia</i> 6:291 (1971)
34	<i>B. fasciculatus</i> C. Presl var. <i>fallax</i> Maire	<i>Contr.Fl.Afr.Nord:</i> 3427 (1942)
35	<i>B. fasciculatus</i> C. Presl var. <i>flavascens</i> Lojac	<i>Fl.Sicul.</i> 3:355 (1909)
36	<i>B. fasciculatus</i> C. Presl var. <i>multiflorus</i> Lojac	<i>Fl.Sicul.</i> 3:355 (1909)

NO	NAMES	PLACE OF PUBLICATION
37	<i>B. fasciculatus</i> C. Presl f. <i>parlatori</i> Pamp.	<i>Archiv.Bot.</i> 12:18 (1936)
38	<i>B. fasciculatus</i> C. Presl f. <i>pubescens</i> Pamp.	<i>Archiv.Bot.</i> 12:21 (1936)
39	<i>B. fasciculatus</i> C. Presl var. <i>tenuiflorus</i> (Viv.) Beg. & Vacc.	<i>Contr.Fl.Libia</i> 35 (1912)
40	<i>B. flabellatus</i> Hack. ex Boiss.	<i>Fl.Orient.</i> 5:648 (1884)
41	<i>B. flavescens</i> Tausch.	<i>Flora (Regensb.)</i> 20:124 (1837)
42	<i>B. grandiflorus</i> Weig.	<i>Obs.Bot.</i> 9 (1772)
43	<i>B. gussonii</i> Parl.	<i>Rar.Fl.Sic.</i> 2:8 (1840)
44	<i>B. gussonii</i> Parl. var. <i>boraei</i> (Jord.) Fouillade	<i>Bull.Soc.Bot.France</i> 80:482 (1933)
45	<i>B. gussonii</i> Parl. var. <i>rigidus</i> (Roth) Lindberg	<i>Act.Soc.Sci.Fenn.n.ser B</i> 12:15 (1932)
46	<i>B. gussonii</i> Parl. var. <i>secundus</i> Cugnac & A. Camus	<i>Bull.Soc.Bot.Fl.</i> 78:338, pl.5, f.4 (1931)
47	<i>B. gynandrus</i> Roth	<i>Cat.Bot.I.</i> :15 (1797)
48	<i>B. haussknechtii</i> Boiss.	<i>Fl.Orient.</i> 5:648 (1884)
49	<i>B. incrassatus</i> Lam.	<i>Encycl.</i> 1:469 (1785)
50	<i>B. jubatus</i> Ten.	<i>Fl.Napol.</i> 3:89 (1820)
51	<i>B. jubatus</i> Vill.	<i>Hist.Pl.Dauph.</i> 2:118 (1787)
52	<i>B. krausei</i> Begl.	<i>Acta Hort.Petrop.</i> 7:600 (1881)
53	<i>B. longearistatus</i> Gilib.	<i>Exerc.Phyt.</i> 2:536 (1792)
54	<i>B. longipilus</i> Kumm. & Sendtn.	<i>Flora</i> 32: 757 (1849)
55	<i>B. macrantherus</i> Hack. ex Trab.	<i>Batt. & Trab., Fl.Alger.</i> 2:(Monoc.) 226 (1895)
56	<i>B. madritensis</i> L.	<i>Cent.Pl.</i> 1:5 (1755)
57	<i>B. madritensis</i> Cav. ex Kunth	<i>Enum.Pl.</i> 1: 419 (1833)

NO	NAMES	PLACE OF PUBLICATION
58	<i>B. madritensis</i> L. var. <i>ambigens</i> Coss. & Dur.	<i>Expl.Sci., Alger.</i> 2:158 (1855)
59	<i>B. madritensis</i> L. var. <i>caucasicus</i> Hack. & Fedtsch.	<i>Bull.Gard.Bot.Pierre Grand</i> 14 (Suppl. 2):89 (1915)
60	<i>B. madritensis</i> L. var. <i>ciliatus</i> Guss.	<i>Fl.Sic.Syn.</i> 1:78 (1843)
61	<i>B. madritensis</i> L. f. <i>ciliatus</i> Guss.	<i>Fl.Sic.Syn.</i> 1:78 (1843)
62	<i>B. madritensis</i> L. var. <i>curtisii</i> Bab. ex Syme	<i>Sowerby, Engl.Bot.</i> ed.3 11:161 (1873)
63	<i>B. madritensis</i> L. ssp. <i>delilei</i> (Boiss.) Maire & Weiller	<i>Maire, Contr.Fl.Afr.Nord.:</i> 2874 (1939)
64	<i>B. madritensis</i> L. ssp. <i>delilei</i> (Boiss.) Maire & Weiller var. <i>glabriglumis</i> Maire & Weiller	<i>Maire, Contr.Fl.Afr.Nord.:</i> 2874 (1939)
65	<i>B. madritensis</i> L. ssp. <i>delilei</i> (Boiss.) Maire & Weiller var. <i>villiglumis</i> Maire & Weiller	<i>Maire, Contr.Fl.Afr.Nord.:</i> 2874 (1939)
66	<i>B. madritensis</i> L. var. <i>delilei</i> Boiss.	<i>Fl.Orient.</i> 5: 649 (1884)
67	<i>B. madritensis</i> L. var. <i>diandrus</i> (Curtis) Hook. f.	<i>Stud.Fl.Brit.Isles</i> 450 (1870)
68	<i>B. madritensis</i> L. ssp. eu- <i>madritensis</i> Maire & Weiller var. <i>ambigens</i> Coss. & Dur.	<i>Expl.Sc.Alg.:</i> 158 (1856)
69	<i>B. madritensis</i> L. ssp. eu- <i>madritensis</i> Maire & Weiller var. <i>ciliatus</i> Guss.	<i>Dubnis & Faurel, Bull.Soc.Hist.</i> <i>Nat.Afr.Nord.</i> 48: 483 (1957)
70	<i>B. madritensis</i> L. ssp. eu- <i>madritensis</i> Maire & Weiller var. <i>glabriculumis</i> Maire & Weiller	<i>Jahandiez & Maire, Cat.Maroc.:</i> 943 (1941)
71	<i>B. madritensis</i> L. ssp. eu- <i>madritensis</i> var. <i>pubiculumis</i> Maire & Weiller	<i>Maire, Fl.Afric.Nord</i> 3: 238 (1955)

NO	NAMES	PLACE OF PUBLICATION
72	<i>B. madritensis</i> L. ssp. eu- <i>madritensis</i> Maire & Weiller var. <i>victorini</i> Maire	<i>Jahandiez & Maire, Cat. Maroc.: 943 (1941)</i>
73	<i>B. madritensis</i> L. var. <i>genuinus</i> Willk.	<i>Prod.Fl.Hisp. 1:99 (1861)</i>
74	<i>B. madritensis</i> L. var. <i>glabriglumis</i> Maire & Weiller	<i>Cat.Plantes Maroc IV:943 (1941)</i>
75	<i>B. madritensis</i> L. var. <i>maximus</i> (Desf.) St Amans	<i>Fl.Agen.: 45 (1821)</i>
76	<i>B. madritensis</i> L. var. <i>monandrus</i> Guss.	<i>Fl.Sic.Syn. 1:78 (1843)</i>
77	<i>B. madritensis</i> L. f. <i>persterilis</i> A. de Cugnac & A. Camus	<i>Bull.Soc.Bot.Fr. 78:340 (1931)</i>
78	<i>B. madritensis</i> L. var. <i>pubescens</i> sensu Anth.	<i>Notes Roy.Bot.Gard.Edinb. 18:302 (1935)</i>
79	<i>B. madritensis</i> L. var. <i>purpurascens</i> (Del.) Post	<i>Fl.Syria, Palest. and Sinai, ed. 1:892 (1896)</i>
80	<i>B. madritensis</i> L. var. <i>purpurens</i> Lojac	<i>Fl.Sicul. 3:353 (1909)</i>
81	<i>B. madritensis</i> L. var. <i>rigidus</i> (Roth) Bab. ex Syme	<i>Sowerby, Engl.Bot. ed. 3.11:61 (1873)</i>
82	<i>B. madritensis</i> L. ssp. <i>rubens</i> (L.) Husnot	<i>Gram.Fr.Belg. 71 (1899)</i>
83	<i>B. madritensis</i> L. var. <i>villosissimus</i> Maire	<i>Maire, Contr.Fl.Afr.Nord.: 2372 (1937)</i>
84	<i>B. madritensis</i> L. var. <i>victorinii</i> (Sennen & Mauricio) Maire	<i>Emberger & Maire, Cat.Pl.Maroc 4: 943 (1941)</i>
85	<i>B. madritensis</i> L. x <i>maximus</i> A. Camus	<i>Bull.Soc.Bot.Fr. 76:596 (1929)</i>
86	<i>B. madritensis</i> L. x <i>sterilis</i> A. de Cugnac & A. Camus	<i>Bull.Soc.Bot.Fr. 78:339 (1931)</i>

NO	NAMES	PLACE OF PUBLICATION
87	<i>B. madritensis</i> L. x <i>tectorum</i> A. Camus	<i>Bull.Soc.Bot.Fr.</i> 78:101 pl.5 f. 1 (1931)
88	<i>B. maximus</i> Desf.	<i>Fl.Atlant.</i> 1:95. pl.26 (1798)
89	<i>B. maximus</i> Gilib.	<i>Exerc.Phyt.</i> 2:535 (1792)[? nom. illegit.]
90	<i>B. maximus</i> Presl	[not traced]
91	<i>B. maximus</i> Desf. var <i>ambigens</i> (Jord.) Asch. & Graebn.	<i>Syn.Mittleleur.Fl.</i> 2(1): 595 (1903)
92	<i>B. maximus</i> Desf. var. <i>biramosus</i> Vayreda	<i>Cavanillesia</i> 4:62 (1931)
93	<i>B. maximus</i> Desf. var. <i>glabra</i> Willk.	<i>Willk. & Lange, Prod.Fl.Hisp.</i> 1:98 (1861)
94	<i>B. maximus</i> Desf. var. <i>gussonii</i> (Parl.) Parl.	<i>Fl.Ital.</i> 1:407 (1848)
95	<i>B. maximus</i> Desf. var. <i>minor</i> Boiss.	<i>Voy.Bot.Esp.</i> 2:677 (1839-45)
96	<i>B. maximus</i> Desf. var. <i>pilosus</i> (Dietr.) Richt.	<i>Pl.Eur.</i> 1:114 (1890)
97	<i>B. Moeszii</i> Penzes	<i>Magyar Bot.Lapok.</i> 33:24. pl.10 (1934)
98	<i>B. multispicatus</i> Rte.	<i>Sch.Syst.</i> II:650 (1817)
99	<i>B. muralis</i> Huds.	<i>Fl.Angl.</i> 50 (1762)
100	<i>B. ovatus</i> Gaertn.	<i>Nov.Comm.Acad.Petrop.</i> XIV:537 (1770)
101	<i>B. pilosus</i> F.G.Dietr.	<i>Volst.Lex.Gaertn.Bot.</i> 1:558 (1802)
102	<i>B. polystachyus</i> D.C.	<i>Lam. & DC., Fl.Fr.</i> ed.3.5: 276 (1815)
103	<i>B. propendens</i> Jord.	<i>Billot, Annot.Fl.Fr. & Allem.</i> 231 (1855)
104	<i>B. rigens</i> L.	<i>Mant. I,</i> 33 (1767)
105	<i>B. rigens</i> Vaud.	<i>Roem., Script.Pl.Hisp.</i> 49 (1796)
106	<i>B. rigens</i> L. var. <i>gussonii</i> (Parl.) Dur. & Schinz	<i>Consp.Fl.Afr.</i> 5:926 (1894)

NO	NAMES	PLACE OF PUBLICATION
107	<i>B. rigens</i> L. ssp. <i>macrantherus</i> (Hack.) A. Fernandes, J. Garcia & R. Fernandes	<i>Mem.Soc.Brot.</i> 4:27 (1948)
108	<i>B. rigidus</i> Roth	<i>Bot.Mag.(Zürich)</i> 4(10):21 (1790)
109	<i>B. rigidus</i> Reichb.	<i>Ic.Fl.Germ.</i> 1:41 (1850)
110	<i>B. rigidus</i> Roth ex. Reichb.	<i>Icon.Fl.Germ.Helv.</i> 1:31.n.1586 (1834)
111	<i>B. rigidus</i> C.A. Mey.	<i>Mey.,Verz.Pfl.Cauc.</i> 23 (1831)
112	<i>B. rigidus</i> Roth var. <i>gussonii</i> (Parl.) Coss. & Dur.	<i>Expl.Sci.Alger.</i> 2:159 (1855)
113	<i>B. rigidus</i> Roth ssp. <i>gussonei</i> (Parl.) Maire	<i>Cuenod, Flore Tunisie</i> 144 (1954)
114	<i>B. rigidus</i> Roth ssp. <i>gussonii</i> (Parl.) Maire var. <i>gussonii</i> (Parl.) Maire & Weiller	<i>Maire, Fl.Afrique Nord</i> 3:234 (1955)
115	<i>B. rigidus</i> Roth ssp. <i>gussonii</i> (Parl.) Maire var. <i>gussonii</i> (Parl.) Maire & Weiller f. <i>propendens</i> (Jord.) Maire & Weiller	<i>Maire, Fl.Afrique Nord</i> 3:235 (1955)
116	<i>B. rigidus</i> Roth ssp. <i>gussonii</i> (Parl.) Maire var. <i>macrantherus</i> (Hackel) Maire & Weiller ex. Lainz	<i>Anal.Inst.Bot.Cavanilles</i> 14:554 (1956)
117	<i>B. rigidus</i> Roth var. <i>gracilis</i> Cugnac	<i>Bull.Soc.Bot.Fr.</i> 78:338, pl.5, f. 3 (1931)
118	<i>B. rigidus</i> Roth ssp. <i>maximus</i> (Desf) Rothm. & Silva	<i>Agron.Lusit.</i> 1:248 (1939)
119	<i>B. rigidus</i> Roth ssp. <i>maximus</i> (Desf.) Rothm. & Silva var. <i>ambigens</i> (Jord.) Maire & Weiller	<i>Maire, Fl.Afrique Nord</i> 3:234 (1955)

NO	NAMES	PLACE OF PUBLICATION
120	<i>B. rigidus</i> Roth ssp. <i>maximus</i> (Desf.) Rothm. & Silva var. <i>minor</i> (Boiss.) Maire	<i>Cat.Plantes du Maroc</i> IV:943 (1941)
121	<i>B. rigidus</i> Roth var. <i>minor</i> (Boiss.) Maire	<i>Cat.Plantes du Maroc</i> IV:943 (1941)
122	<i>B. rochelianus</i> Opiz.	<i>Nat.Bei tr.z.Naturg.</i> 9:119 (1925)
123	<i>B. rubens</i> L.	<i>Cent.Pl.</i> 1:5 (1755)
124	<i>B. rubens</i> "Syst.Veg. ex Cav.ic" ex Host	<i>Icon.Gram.Austr.</i> 1:pl.18 (1801)
125	<i>B. rubens</i> "L.Sibth.Flor. Graec." ex Delile	<i>Descr.Egypte</i> 2:52 (1812)
126	<i>B. rubens</i> Desf.	<i>Fl.Anjou</i> 63 (1827)
127	<i>B. rubens</i> L. var. <i>Borosii</i> Penz.	<i>Bot.Kozlém.</i> 33:126.f. x.49.d (1936)
128	<i>B. rubens</i> L. ssp. eu- <i>rubens</i> Maire var. <i>canescens</i> (Viv.) Pamp.	<i>B.Soc.Bot.Ital.</i> :79 (1914)
129	<i>B. rubens</i> L. ssp. <i>fasciculatus</i> (Presl) Trabut	<i>Batt. & Trab., Fl.Alger.Mon.</i> 226 (1895)
130	<i>B. rubens</i> L. ssp. <i>fasciculatus</i> (Presl) Trabut var. <i>alexandrinus</i> (Thell.) Maire & Weiller	Maire, <i>Fl.Afrique Nord</i> 3:242 (1955)
131	<i>B. rubens</i> L. ssp. <i>fasciculatus</i> (Presl) Trabut var. <i>ambigens</i> Maire	<i>Bull.Soc.Hist.Nat.Afrique Nord</i> 34: 141 (1943)
132	<i>B. rubens</i> L. ssp. <i>fasciculatus</i> (Presl) Trabut var. eu- <i>fasciculatus</i> Maire & Weiller	<i>Bull.Soc.Hist.Nat.Afrique Nord</i> 311: (1939)
133	<i>B. rubens</i> L. ssp. <i>fasciculatus</i> (Presl) Trabut var. <i>fallax</i> Maire	<i>Bull.Soc.Hist.Nat.Afrique Nord</i> 3427: (1942)

NO	NAMES	PLACE OF PUBLICATION
134	<i>B. rubens</i> L. ssp. <i>fasciculatus</i> (Presl) Trabut var. <i>puberulus</i> Maire & Weiller	<i>Bull.Soc.Hist.Nat.Afrique Nord</i> 30: 310 (1939)
135	<i>B. rubens</i> L. var. <i>fasciculatus</i> Mutel	<i>Fl.Franc.</i> 4:133 (1837)
136	<i>B. rubens</i> L. var. <i>glabellus</i> Maire	<i>Bull.Soc.Hist.Nat.Afrique Nord</i> 25: 325 (1934)
137	<i>B. rubens</i> L. var. <i>glabiglumis</i> Maire	<i>Cat.Plantes Maroc</i> 4:943 (1941)
138	<i>B. rubens</i> L.f. <i>intermedius</i> Pamp.	<i>Bull.Soc.Bot.Ital.</i> 11 (1915)
139	<i>B. rubens</i> L. var. <i>maximus</i> (Desf.) Fiori	<i>Fl.Anal.Ital.</i> 1:99 (1896)
140	<i>B. rubens</i> L. var. <i>polystachius</i> (DC) Mutel	<i>Fl.Franc.</i> 4:133 (1837)
141	<i>B. rubens</i> L. var. <i>typicus</i> Fiori	<i>Nuov.Fl.Anal.Ital.</i> 149 (1923)
142	<i>B. rubens</i> L. x <i>tectorum</i> A. Camus	<i>Bull.Soc.Bot.Franc.</i> 80:39 (1933)
143	<i>B. rubens</i> L. c. <i>rigidus</i> (Roth.) Mutel	<i>Fl.Franc.</i> 4:133 (1837)
144	<i>B. scaberrimus</i> Ten.	<i>Fl.Nap.</i> 3:89 (1820)
145	<i>B. scaberrimus</i> St.-Lager	<i>Rech.Hist.</i> 43 (1884)
146	<i>B. sericeus</i> Drobov	<i>Feddes Repert.</i> 21:39 (1925)
147	<i>B. sericeus</i> Ten.	<i>Fl.Nap.Prod.</i> 10 (1820)
148	<i>B. setaceus</i> Buckl.	<i>Prod.Acad.Nat.Sci.Philad.</i> 1862: 98 (1862)
149	<i>B. sterilis</i> L.	<i>Sp.Pl.</i> 77 (1753)
150	<i>B. sterilis</i> Guss.	<i>Suppl.Fl.Sic.Prodr.</i> 1:27 (1832)
151	<i>B. sterilis</i> Lange	<i>Kumm. & Seudtn. Flora</i> 32:758 (1849)
152	<i>B. sterilis</i> L. var. <i>arrectus</i>	<i>Schur.Enum.Pl.Transsilv.</i> : 805 (1866)

NO	NAMES	PLACE OF PUBLICATION
153	<i>B. sterilis</i> L.f. <i>diandrus</i> (Curtis) Kuntze	<i>Act.Hort.Petrop.</i> 10:251 (1887)
154	<i>B. sterilis</i> L. var. <i>fasciculatus</i> (Presl) Kuntz	<i>Act.Hort.Petrop.</i> 10:251 (1887)
155	<i>B. sterilis</i> L.f. <i>glaberrimus</i> Soó	<i>Acta Bot.Acad.Sci.Hung.</i> , 17(1-2): 115 (1972)
156	<i>B. sterilis</i> L. var. <i>glabrescens</i> Zapal	<i>Consp.Fl.Galic.Crit.Rozpr.Wydz.Mat.</i> <i>Przyr.Akad.Umiejetn.Krakow</i> III. 4, B. 188 (1904)
157	<i>B. sterilis</i> L.f. <i>hirsutior</i> Waisbecker	<i>Oesterr.Bot.Zeitschr.</i> 51:127 (1901)
158	<i>B. sterilis</i> L. subvar. <i>inops</i> Beck f. <i>intermedius</i> Reichb.	<i>Fl.Germ.</i> 1:42 (1830)
159	<i>B. sterilis</i> L. var. <i>intermedius</i> Reichb.	<i>Fl.Germ.</i> 1:42 (1830)
160	<i>B. sterilis</i> L. var. <i>krausei</i> Kuntze	<i>Act.Hort.Petrop.</i> 10:249,250 (1887)
161	<i>B. sterilis</i> L. var. <i>madritensis</i> (L.) Kuntze	<i>Act.Hort.Petrop.</i> 10:250 (1887)
162	<i>B. sterilis</i> L. var. <i>maximus</i> (Desf.) Kuntze	<i>Act.Hort.Petrop.</i> 10:250 (1887)
163	<i>B. sterilis</i> L. f. <i>nanus</i> Bolzon	<i>Nuov.Giorn.Bot.Ital.N.Ser.</i> 20:316 (1913)
164	<i>B. sterilis</i> L. var. <i>normalis</i> Kuntze	<i>Act.Hort.Petrop.</i> 10:249, 250 (1887)
165	<i>B. sterilis</i> L. var. <i>nudus</i> (Klett. & Richt.) Kuntze	<i>Act.Hort.Petrop.</i> 10:250 (1887)
166	<i>B. sterilis</i> L. var. <i>oligostachyus</i> Aschers. & Graebn.	<i>Syn.Mitteleur.Fl.</i> 2:592 (1901)
167	<i>B. sterilis</i> L. var. <i>pilosus</i> Rohl.	<i>Sitzungs.Böhm.Ges.Wiss.Math.Nat.Cl.</i> [pt] 39:31 (1902)
168	<i>B. sterilis</i> L. f. <i>ponticus</i> (Koch) Kuntze	<i>Act.Hort.Petrop.</i> 10:251 (1887)

NO	NAMES	PLACE OF PUBLICATION
169	<i>B. sterilis</i> L. var. <i>pubescens</i> (Aschs.) Kuntze	<i>Act.Hort.Petrop.</i> 10:251 (1887)
170	<i>B. sterilis</i> L. var. <i>purpureus</i> Schur.	<i>Enum.Pl.Transsilv.</i> :805 (1866)
171	<i>B. sterilis</i> L. var. <i>rigidus</i> (Roth) Kuntze	<i>Act.Hort.Petrop.</i> 10:251 (1887)
172	<i>B. sterilis</i> L. var. <i>rubens</i> (L.) Kuntze	<i>Act.Hort.Petrop.</i> 10:249-251 (1887)
173	<i>B. sterilis</i> L. var. <i>scaberrimus</i> (Ten.) Fiori	<i>Fl.Anal.Ital.</i> 1:99 (1896)
174	<i>B. sterilis</i> L. var. <i>tectorum</i> (L.) Kuntze	<i>Act.Hort.Petrop.</i> 10:250 (1887)
175	<i>B. sterilis</i> L. var. <i>trichanthus</i> Kuntze	<i>Act.Hort.Petrop.</i> 10:250 (1887)
176	<i>B. sterilis</i> L. var. <i>typicus</i> Fiori	<i>Nuov.Fl.Anal.Ital.</i> 147 (1923)
177	<i>B. sterilis</i> L. var. <i>validus</i> Zapal	<i>Consp.Fl.Galic.Crit.</i> , Rozyr.Wydz. <i>Mat.-Przyr.Akad.Umiejtn.Krakow</i> III. 4,B.188 (1904)
178	<i>B. sterilis</i> L. f. <i>varius</i> (Brot.) Kuntze	<i>Act.Hort.Petrop.</i> 10:251 (1887)
179	<i>B. sterilis</i> L. var. <i>velutinus</i> Volk ex Hegi	<i>Illustr.Fl.Mittelur.</i> 1:362 (1908)
180	<i>B. sterilis</i> L. var. <i>viridis</i> Schur.	<i>Enum.Pl.Transsilv.</i> :805 (1866)
181	<i>B. sterilis</i> L. x <i>tectorum</i> Guétrot ex A. Camus	<i>Bull.Soc.Bot.Fr.</i> 91:79 (1944)
182	<i>B. tectorius</i> Dulac.	<i>Fl.Haut.Pyr.</i> 96 (1867)
183	<i>B. tectorum</i> L.	<i>Sp.Pl.</i> 77 (1753)
184	<i>B. tectorum</i> L. var. <i>abortiflorus</i> (St. Amans) Richt	<i>Pl.Eur.</i> 1:117 (1890)
185	<i>B. tectorum</i> L. var. <i>anisantha</i> Hackel	<i>Denk-Schr.Math.-nat.Kl.Akad.Wiss.</i> <i>Wien</i> 50:10,77 (1885)

NO	NAMES	PLACE OF PUBLICATION
186	<i>B. tectorum</i> L. var. <i>australis</i> (St. Amans) Gren. & Godr.	<i>Fl.France</i> 3:583 (1856)
187	<i>B. tectorum</i> L. var. <i>floridus</i> Gremli	<i>Excurs.Schweiz.ed.</i> 9:438 (1901)
188	<i>B. tectorum</i> L. var. <i>genuinus</i> Gren. & Godr.	<i>Fl.France</i> 3:583 (1856)
189	<i>B. tectorum</i> L. var. <i>glabratus</i> Spenner	<i>F.Friburg.</i> 1:152 (1825)
190	<i>B. tectorum</i> L. var. <i>glabratus</i> Schuebl. & Marteus	<i>Fl.Württemberg</i> 87 (1834)
191	<i>B. tectorum</i> L. var. <i>glabratus</i> Hartn.	<i>Handb.Skand.Fl.</i> ed.4. 40 (1843)
192	<i>B. tectorum</i> L. var. <i>glabratus</i> Sond.	<i>Fl.Hamburg.</i> 71 (1851)
193	<i>B. tectorum</i> L. var. <i>glabratus</i> Celak.	<i>Prod.Fl.Böhm.</i> 726 (1881)
194	<i>B. tectorum</i> L. var. <i>glaber</i> Coss. & Germ.	<i>Fl.Env.Paris</i> 2:653 (1845)
195	<i>B. tectorum</i> L. var. <i>glaber</i> Ducomm.	<i>Taschenb.Schweiz.Bot.</i> 884 (1869)
196	<i>B. tectorum</i> L. subvar. <i>glaber</i> Cheval	<i>Fl.Envir.Paris</i> ed.2. 831 (1861)
197	<i>B. tectorum</i> L. var. <i>grandiflorus</i> Hack. ex Fedtsch.	<i>Bull.Gard.Bot.Pierre Grand</i> 14 (Suppl.2):89 (1915)
198	<i>B. tectorum</i> L. var. <i>hirsutus</i> Regel	<i>Acta Hort.Petrop.</i> 7:600 (1881)
199	<i>B. tectorum</i> L. var. <i>longipila</i> Borb. ex Fedtsch.	<i>Bull.Gard.Bot.Pierre Grand</i> 14 (Suppl.2): 89 (1915)
200	<i>B. tectorum</i> L. var. <i>longipilus</i> (Kum. & Sendtn.) Richt.	<i>Pl.Eur.</i> 1:114 (1890)
201	<i>B. tectorum</i> L. var. <i>longipilus</i> (Kum. & Sendtn.) Borb.	<i>Földm.</i> 11 (1882)

NO	NAMES	PLACE OF PUBLICATION
202	<i>B. tectorum</i> L. var. <i>nudus</i> Klett. & Richt.	<i>Fl. Leipz.</i> 109 (1830)
203	<i>B. tectorum</i> L. f. <i>nudus</i> (Klett. & Richt.) Hiitnen	<i>Suomen Kasvis</i> 220 (1933)
204	<i>B. tectorum</i> L. var. <i>oligostachys</i> Podpera	<i>Kvetena Moravy</i> 6:57 (1926)
205	<i>B. tectorum</i> L. var. <i>pauciflorus</i> Lindem. ex Fedtsch.	<i>Bull. Gard. Bot. Pierre Grand</i> 14 (Suppl. 2): 89 (1915)
206	<i>B. tectorum</i> L. var. <i>ponticus</i> (C. Koch) Aschers. & Graebn.	<i>Syn. Middleleurl. Fl.</i> 2:594 (1901)
207	<i>B. tectorum</i> L. var. <i>pubescens</i> Schur.	<i>Enum. Pl. Transsilv.</i> 805 (1866)
208	<i>B. tectorum</i> L. var. <i>purpurascens</i> Linden. ex Fedtsch.	<i>Bull. Gard. Bot. Pierre Grand</i> 14 (Suppl. 2): 89 (1915)
209	<i>B. tectorum</i> L. var. <i>rubescens</i> Roch.	<i>Reise</i> p. 40
210	<i>B. tectorum</i> L. var. <i>robustus</i> Zapal.	<i>Consp. Fl. Gal. Critic.</i> 1:76 (1906)
211	<i>B. tectorum</i> L. var. <i>sirjaevii</i> Podp.	<i>Fl. v. Mähren</i> 6:57 (1926)
212	<i>B. tectorum</i> L. var. <i>spiculis-scabris</i> Mert. & Koch. ex Grun.	<i>Bull. Soc. Nat. Moscow</i> 42:134 (1869)
213	<i>B. tectorum</i> L. var. <i>spiralis</i> Hack.	<i>Denkschr. math.-nat. Kl. Akad. Wiss.</i> <i>Wien</i> 50:10, 77 (1885)
214	<i>B. tectorum</i> L. subvar. <i>tectorum</i> f. <i>longipilus</i> (Kumm. & Sendtn.) Borb.	<i>Földen.</i> 11 (1882)
215	<i>B. tectorum</i> L. subvar. <i>tectorum</i> f. <i>nudus</i> (Klett. & Richt.) St. John	<i>Fl. Southeast Washington & Adj. Idaho</i> 36 (1937)
216	<i>B. tectorum</i> L. var. <i>triflorus</i> G. Meyer	<i>Chloris Hanov.</i> 618 (1836)

NO	NAMES	PLACE OF PUBLICATION
217	<i>B. tectorum</i> L. var. <i>umbrosus</i> Borbás	<i>Math.Termesz.Közlem.</i> 15:339 (1878)
218	<i>B. tectorum</i> L. var. <i>velutinus</i> Ducomm.	<i>Taschenb.Schweiz.Bot.</i> 884 (1869)
219	<i>B. tectorum</i> L. var. <i>villosus</i> G. Meyer	<i>Chloris Hanov.</i> 618 (1836)
220	<i>B. tectorum</i> L. var. <i>virens</i> Griseb.	<i>Spicil.Pl.Rumel.</i> 2:449 (1844)
221	<i>B. tectorum</i> L. var. <i>vulgaris</i> Spenner	<i>Fl.Friburg.</i> 1:152 (1825)
222	<i>B. varius</i> Brot.	<i>Fl.Lusit.I:</i> 113 (1804)
223	<i>B. villosus</i> Forsk.	<i>Fl.Aegypt.Arab.</i> 23 (1775)
224	<i>B. villosus</i> Scop.	<i>Fl.Carn. ed.2.1:</i> 83 (1772)
225	<i>B. villosus</i> Suter.	<i>Fl.Helv.</i> 1:62 (1802)
226	<i>B. villosus</i> K. Gruel.	<i>F.Badens.</i> 1:229 (1805)
227	<i>B. tectorum</i> Forsk. var. <i>ambigens</i> (Jord.) Aschers. & Graebn.	<i>Syn.Mitteleur.Fl.</i> 2:595 (1901)
228	<i>B. villosus</i> Forsk. ssp. en- <i>villosus</i> Maire ex Jah. ex Maire	<i>Cat.Pl.Maroc.</i> 1:80 (1931)
229	<i>B. villosus</i> Forsk. ssp. <i>gussonei</i> (Parl.) Holmboe	<i>Veg.Cypr.</i> 37 (1914)
230	<i>B. villosus</i> Forsk. var. <i>gussonei</i> (Parl.) Aschers. & Graebn.	<i>Syn.Mitteleur.Fl.</i> 2:595 (1901)
231	<i>B. villosus</i> Forsk. var. <i>maximus</i> (Desf.) Aschers. & Graebn.	<i>Syn.Mitteleur.Fl.</i> 2:595 (1901)
232	<i>B. villosus</i> Forsk. var. <i>rigidus</i> (Roth) Aschers. & Graebm.	<i>Sym.Mitteleur.Fl.</i> 2:596 (1901)
233	<i>Festuca madritensis</i> Desf.	<i>Fl.Atl.</i> 1:91 (1798)
234	<i>Festuca rubens</i> Pers.	<i>Syn.</i> 1:94 (1805)

NO	NAMES	PLACE OF PUBLICATION
235	<i>Schedonorus sterilis</i> (L.) Fries	<i>Bot.Not.</i> 131 (1843)
236	<i>Schedonorus tectorum</i> (L.) Fries	<i>Bot.Not.</i> 131 (1843)
237	<i>Triniusia flavescens</i> Steud.	<i>Syn.Pl.Glum.</i> 1:328 (1854)
238	<i>Zerna gussonii</i> (Parl.) Grossh.	<i>Trudy Bot.Inst.Azerbaidzh.Fil.</i> <i>Akad.Nauk.SSSR.</i> 8:305 (1939)
239	<i>Zena madritensis</i> (L.) S.F. Gray	<i>Nat.Arrang.Brit.Pl.</i> 2:117 (1821)
240	<i>Zena rubens</i> (L.) Grossh.	<i>Trudy Bot.Inst.Azerbaidzh.Fil.</i> <i>Akad.Nauk.SSSR.</i> 8:306 (1939)
241	<i>Zena sterilis</i> (L.) Panzer	<i>Denkschr.Muench.</i> 1813:297 (1814)
242	<i>Zena tectorum</i> (L.) Panz.	<i>Denkschr.Muench.</i> 1813:297 (1814)
A.	<i>B. fasciculatus</i> C. Presl. subsp. <i>delilei</i> (Boiss.) H. Scholz	<i>Willdenowia</i> 6:291 (1971)
B.	<i>B. madritensis</i> L. subsp. <i>kunkelii</i> H. Scholz	<i>Willdenowia</i> 11:251 (1981)
C.	<i>B. tectorum</i> L. subsp. <i>lucidus</i> Sales	in <i>Contrib.Sel.Fl.Veg.Orientis</i> (1991) - in press.
D.	<i>B. diandrus</i> Roth. var. <i>rigidus</i> (Roth) Sales	not yet in press

Appendix 4.1 List of the reagents and their method of preparation used in chromosome studies with reference to proprietary sources of chemicals in brackets where helpful.

- 1) 1-Bromonaphthalene [BDH]. Saturate aqueous solution.
- 2) 8-Hydroxyquinoline [Griffin & George]. 0.002M aqueous solution.
- 3) P-Dichlorobenzene [May & Baker]. Saturated aqueous solution.
- 4) Carnoy's fixative. 6(ethanol):3(acetic acid):1(chloroform). Must be prepared fresh.
- 5) Farmer's fixative. 3(ethanol):1(acetic acid).
- 6) Lacto-propionic orcein. Stock solution: 2g natural orcein [Sigma 03626] dissolved overnight in a mixture of 50ml lactic acid and 50ml propionic acid. Filter. Working solution: dilute stock solution to 45% with water.
- 7) Acid acetic orcein. 1(HCl):9(acetic orcein). Must be prepared fresh.
- 8) Feulgen's stain:
 - A. Add 0.7g basic fuchsin [BDH/GURR 34088] and 3.8g sodium metabisulphate to 200ml of 0.15N HCl.
 - B. Place mixture on a magnetic stirrer for 2-3 hours at room temperature. At the end of this period, the solution should be straw-coloured.
 - C. Decolourize with 1g activated charcoal by shaking.
 - D. Filter and make up to 200ml with distilled water. The solution should be as clear as water.
 - E. The pH of the solution should be about 2.2
 - F. Store in the fridge in a tightly stoppered bottle.
- 9) SO₂ water. Solution of 5ml 10% potassium metabisulphate (percentage is weight/volume), 5ml N HCl and 100ml distilled water. Must be prepared fresh.
- 10) Cellulase [39074/2C BDH]. Prepare a 4% solution with a piece of Thymol to avoid fungi to grow. Can be used for 1 week.
- 11) Pectinase [2401 Sigma]. Prepare a 4% solution with a piece of Thymol to avoid fungi to grow. Can be used for 1 week.
- 12) Rubber solution [02002 Weldtite].

APPENDIX 5.1.1. Control and data file used in the GENSTAT "Hierarchy" programme; and the produced dendrogram.

GENSTAT V RELEASE 4.04B
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```
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2  'VARI' NUM, A(1...9)$ 120  
3  'SYMMAT' SYM $ 120  
4  'INTEGER' RES $ 120  
5  'INTEGER' TYPO = 9(2)  
6  'INPUT' 2  
7  'READ/P' NUM, A(1...9)  
8  'INPUT' 1  
9  'SMATRIX' SYM; A(1...9); TYPO  
10 'HIERARCHY/CM=4, CT=2.5' SYM; RES  
11 'RUN'
```


APPENDIX 5.1.1. Raw data matrix.

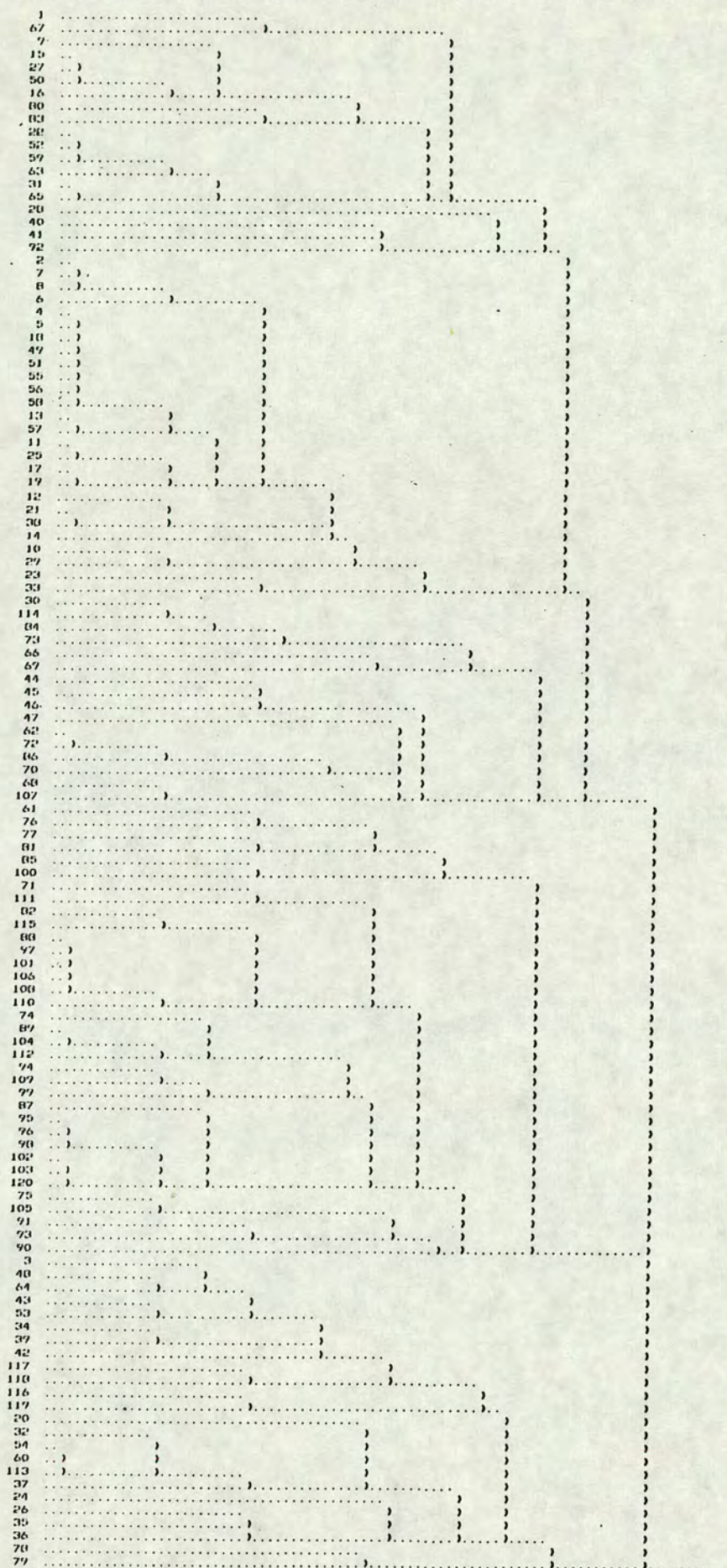
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*** DENDROGRAM ***

LEVELS 100.0 95.0 90.0 85.0 80.0 75.0 70.0 65.0 60.0 55.0 50.0 45.0 40.0 35.0



APPENDIX 5.2.1

Specimens intermediate between

B. diandrus var. *diandrus* and var. *rigidus*

- A. Plants with short branches; callus not much pointed but not round; anthers of var. *diandrus*.

USSR. Azerbaidjan: Baku, Sikh, *Holmberg* 453 (K). South Africa. Cape: Calvinia, *Schmidt* 519A (K).

- B. Anthers very long; callus clearly pointed.

Israel: Philistaeen Plain, Shehunat-Borochoy, 18 iii 1927, *Zeinbrun* s.n. (HUJ). Libya: nr University of Tripoli, sandy barley field, 100m, *Davis* 49454 (E). Morocco: Agadir to Oved Massa, sandy loam, 150m, *Davis* 53768 (E). Tunisia: 10km Soliman to Korbous, wet soil at olive grove, 2N = 42, *Soderstrom* 1437 (K).

- C. Plants with characters of var. *diandrus*, but with very short branches - possibly a result of phenotypic plasticity.

Spain. Sierra de Gredos: El Arenal, 1000m, *Deverall & Flannigan* 0369 (E). Majorca: Palma, 5 v 1903, *White* s.n. (E). USSR. Azerbaidjan: Baku, Tschonig Gorod, *Holmberg* 120 (K). Tunisia: Cornich N of Bizerte, weedy banks by sea, *Davis* 61365 (E).

**A re-assessment of *Bromus tectorum*:
a computer analysis, synaptospermy and chorispermy**

by

Fátima Sales

With 7 figures and 1 table

Abstract

Poaceae

: / Multidisciplinary studies on the *Bromus tectorum* L. complex (~~*Gramineae*~~) throughout its Eurasian distribution resulted in the recognition of two subspecies, the type subspecies and the new ssp. *lucidus* Sales, confined to SW Asia. A computer analysis supported the taxonomy presented. The importance of the number of veins on glumes, synaptospermy and chorispermy in separating the taxa is stressed.

Introduction

t / Plants of the *B. tectorum* L./*B. sericeus* Drobov complex occupy a distinct position in *Bromus* sect. *Genea* because of their elegant/slender, 1-sided panicles, the silvery appearance of the spikelets, the great variation of vein number on the glumes (1, 3, 5 on the lower ones; 3, 4, 5, 7 on the upper ones) and a clear tendency to synaptospermy.

p / c In Eurasia, the area of maximum morphological diversity and probably the centre of origin of the complex, it extends from Macaronesia, throughout Europe, N Africa, SW Asia to the Himalayas, not penetrating deeply into the Arabian Peninsula and becoming very rare in C Asia. It was introduced in N America as early as the 18th century, covering nowadays great stretches of land, especially in the NW being there a noxious, invasive weed. It was introduced as well into Australia and New Zealand probably in the last century; here it is quite rare.

B. tectorum was described from Europe and *B. sericeus* described from Tashkent in Soviet C Asia. The taxa described represent two well-defined extremes of a range of variation. Before the publication of *B. sericeus* in 1925 and even

later, but before the great work that has been done in recent decades on the floras of SW Asia, *B. tectorum* was easily recognised and keyed out from the other *Genea* species.

However, my study of *B. tectorum* and *B. sericeus*, in places where both are likely to occur, has shown a great number and diversity of intermediates for which the existing keys and Floras are, at best, not helpful. As a consequence of this work I have reduced *B. sericeus* Drob. to a subspecies: *B. tectorum* L. ssp. *lucidus* Sales.

History

Prior to the publication of Drob. *Bromus sericeus* in 1925, there is the earlier *B. sericeus* Ten., Fl. Nap. Prod. 1(1): X (1811-15). In the second volume of the same work, Tenore considers his *B. sericeus* a synonym of *B. alopecurus* Poiret (Voy. Barb. 2: 100. 1789) of sect. *Bromus*. The name *B. sericeus* Drob. is thus a later homonym and has to be replaced by a new epithet. It seemed appropriate to adopt the name "lucidus" (= shining) because of the shiny or silvery appearance of the spikelets.

Although distinctive characteristics were well-described and known, the lack of field work in SW Asia deprived taxonomists of a clear idea of the great morphological variation of *B. tectorum* and *B. lucidus*. Drob. in his original description distinguished his new species from *B. tectorum* by the number of veins on glumes, 3 for the lower and 5/7 for the upper, and the much longer spikelets. As time went on, the field work to support the Flora of Turkey, Flora Iranica, Flora of Iraq, Flora of Pakistan, Flora Palaestina and more work in the Arabian Peninsula brought to the attention of taxonomists an increasing number of specimens intermediate between *B. tectorum* and *B. sericeus*. The delimitation between the two taxa became very unclear. The only attempt to solve this taxonomic problem was made by Scholz (1989), who described a new subspecies within *B. sericeus* from Sinai (ssp. *fallax* H. Scholz). Scholz suggested that it might be a hybrid between *B. sericeus* and *B. tectorum*. He drew attention to the synaptospermous condition in *B. sericeus* (the florets do not disarticulate in a spikelet) in contrast to the chorispermy in *B. tectorum*, the consequence of a fully developed callus on the floret base. He described ssp. *fallax* as having a spikelet size intermediate between that of *B. tectorum* and *B. sericeus* and having an incompletely developed callus. I have had the opportunity of studying a very large number of specimens from the whole geographical area of distribution of both taxa and find that the type specimens of ssp. *fallax* represent (in fact, unclear) only one of many morphological variants that can be associated with *B. tectorum*/*B. sericeus*.

Some of the character states used by earlier workers to separate the taxa clearly overlap (e.g. number of spikelets per branch, awn length and anther size) which shows the difficulties in separating the two taxa. The number of veins on glumes was used by all of them. Nevertheless, Nevski (1934), Bor (1968, 1970) and Cope (1982) seem to be aware of some variation in this character. Traditionally *B. tectorum* should have 1/3 veins on glumes and *B. sericeus* 3/5. But, in fact, I have observed specimens designated hitherto as *B. tectorum* with 3, 4 and 5 veins and *B. sericeus* 5 and 7 on the upper glume. As far as lemmas and awns are concerned, only Cope (1982) specified that his measurements refer to the lowermost floret. In fact, lemmas become much shorter towards the top of the rachilla, but awns increase and decrease in length towards the top. Branch length is referred to only by Krechetovich & Vvedensky (1934) in relation to *B. sericeus*. However, particularly in SW Asia and the Canary Islands, ssp. *tectorum* can have shorter branches with very few spikelets. The geographical concentration of these plants in these two areas could be the result of evolutionary tendencies and therefore, have a genetic, selective, basis.

The present analysis

I have considered 38 characters expecting to find some that were more associated with one species than the other. A selection of 9 characters, observed in 120 herbarium specimens, was made for computer analysis. A total of about 1000 specimens of both taxa, and their intermediates, was examined.

B. tectorum designates taller plants, with longer leaves, longer panicles, longer, thinner and more divided panicle branches, and with more spikelets; the spikelets being shorter, less shiny, with fewer florets. Glumes, lemmas, awns, paleas, grains and anthers are all smaller; the lower glume is 1-veined and the upper 3-5-veined. The sterile florets are more clearly separated from the fertile ones by a long rachilla segment. The awn is inserted closer to the lemma apex.

"*B. sericeus*" designates plants that are shorter with regard to the vegetative parts, more robust-looking in reproductive ones, showing bigger structures. Its epithet comes from the more shiny appearance, a consequence of the proportionally larger hyaline margins and paler green colour on the spikelets. The lower glume is 3-veined and the upper 5(-7) veined. The awn extremities are more regular/almost as if cut with scissors at the same level.

Taxonomy

The result of the detailed analysis clearly shows that it is impossible to maintain 2 independent species. Nevertheless, I was convinced that there was some kind of boundary between the two taxa. The characters of greatest importance

were the number of veins on the lower glumes and the dispersal biology, combined to an extent with the geographical distribution and ecology. I consider that the most practical taxonomic resolution of this interesting problem is to recognize two subspecies.

Key to the subspecies

- 1a. Lower glume 1-veined; rachilla callus well-differentiated below each fertile floret (chorispermous plants) (Figs. 1, 2)..... *B. tectorum* ssp. *tectorum*
- b. Lower glume 3-veined; rachilla callus well-differentiated only below the lowermost floret (synaptospermous plants) (Figs. 3, 4)..... *B. tectorum* ssp. *lucidus* Sales

B. tectorum L., Sp. Pl. 77 (1753).

ssp. *tectorum*

Type: Europe. LINN 93/25. - (Smith, 1985, p. 500, designated this specimen as lectotype).

Icon.: Sibthorp & Smith, Fl. Graeca 1: tab. 82 (1806); Hubbard, Grasses, 3rd edit., 62 (1985).

ssp. *lucidus* Sales, nom. et stat. nov. for *B. sericeus* Drobov non Tenore (1811-15)

Type: Syr Darya district, Tashkent, middle part of Keles basin, Kaplanbeck demarcated area, c. 1500 m, 4 v 1921, Abolin 7496 TAK.). Lectotype selected by Tsvelev, Grasses of the Soviet Union 1: 326 (1984).

Icon.: Bor in Townsend & Guest, Fl. Iraq 9: tab. 53 (1968). - as *B. sericeus*.

Ssp. *tectorum* grows up to 4000 m while ssp. *lucidus* is confined to lower lands, up to 1900 m. The former has a large geographical distribution in the Euro-Siberian phytocorion plus an Irano-Turanian component while the second is confined to more arid places in SW Asia (Fig. 5).

A computer analysis of individuals

One hundred and twenty specimens, chosen for computer analysis, covering the total geographical range, were scored for the 9 characters which seemed to me to offer the best means of distinguishing ssp. *tectorum* and ssp. *lucidus* and the various categories of intermediates between them. The characters, character states and 0 1 2 coding are given in Tab. 1. A GENSTAT "Hierarchy" program, UPGMA method, was used and the dendrogram produced is on Fig. 6.

Figs. 1-4. *Bromus tectorum* ssp. *tectorum* and *B. tectorum* ssp. *lucidus*. 1. *B. tectorum* ssp. *tectorum*: side view of top of rachilla-segment of 1st floret connected with the 2nd floret. Callus formed all around the junction between both structures. 2. *B. tectorum* ssp. *tectorum*: abaxial surface of 2nd floret showing callus/scar area; callus well-differentiated. 3. *B. tectorum* ssp. *lucidus*: side view of rachilla segments of 1st floret connected with 2nd floret; callus very incompletely formed between both structures. 4. *B. tectorum* ssp. *lucidus*: adaxial surface of base of 2nd floret showing callus/scar area; callus only partially differentiated; most of the callus/scar area is covered with tissue from the top of the rachilla segment of the 1st floret (bar = 100 μ m).

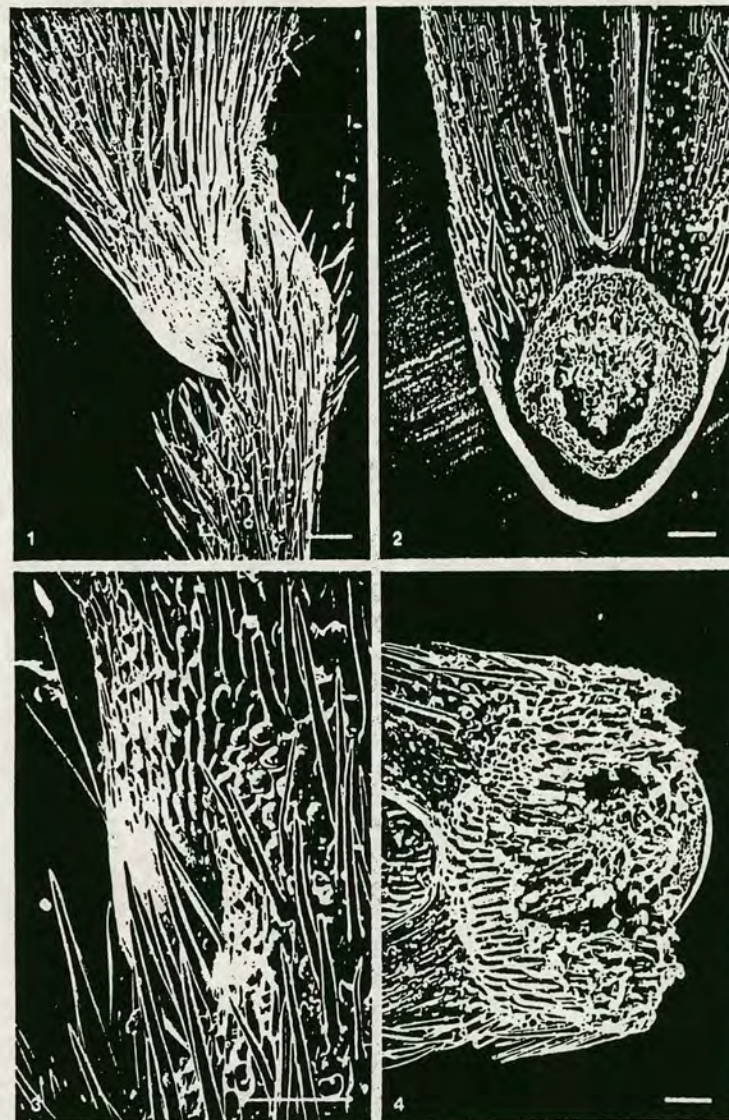




Fig. 5. Distribution of *B. tectorum* in Europe, north Africa and Asia: ssp. *tectorum*; ssp. *lucidus*. The map is based only on specimens studied by the author.

In the dendrogram 3 groups are recognised at a level of 37.5%, each subdivided many times, indicating a high internal variation in each group and considerable overall morphological variation among the individuals studied.

The dendrogram clearly shows that, for the plants analysed, there is no clear-cut difference between the extreme morphologies (i.e. ssp. *tectorum* and ssp. *lucidus*), either from a morphological or geographical viewpoint. However, it points out the existence of those extremes by placing most of the ssp. *lucidus* specimens in one group (B₂) and exclusively in the eastern area of distribution. Therefore, the dendrogram supports my view that subspecific rank is more appropriate for the taxa involved than specific rank.

The dendrogram shows a high morphological variation in the eastern area, with specimens from there distributed throughout the 3 main groups, but it shows also some variation in the west. In group A₂ intermediate specimens from the

Canary Islands are placed together with ssp. *lucidus* from the Arabian Peninsula pointing out the existence of an E-W disjunction of the morphologically intermediate specimens. The dendrogram supports my belief that this disjunction is due to parallel evolution. If the western plants that show intermediate features were relictual, it would be reasonable to expect that these plants would be more concentrated in one of the main groups, and not scattered as they are in the diagram. In addition, if in the west a form of ssp. *lucidus* were relictual, one might expect to find at least a few specimens with its typical morphology; especially in the course of the present comprehensive study.

Tabl. 1. Characters analysed for computer analysis of *B. tectorum* s.l. (including both subspecies). Nine characters were selected from a total of 38 considered. The intermediate range of variation (character state 1) was based on the less frequently occurring variation in both typical extremes. (TE - *B. tectorum* ssp. *tectorum*; LU - *B. tectorum* ssp. *lucidus*).

CHARACTERS	CHARACTER STATE		
	Definitions		
	0 (more like TE)	1 (intermediate)	2 (more like LU)
1. Panicle length (cm)	2.3-21	2.3-8	1-8
2. Panicle branches length	longer than spikelet	same	shorter than spikelet
3. Spikelet length (cm)	1.4-1.9	2-2.5	2.6-3.5
4. No. florets	6-10	11	11-17
5. Disarticulation of spikelet	Yes	-	No
6. Lemma length (mm)	10.5-13.9	14-16	16.1-24
7. Awn length (mm)	12.5-17.4	17.5-18.5	18.6-27
8. Palea length (mm)	8.4-9.4	9.5-10.5	10.6-14
9. No. veins on lower glume	1	-	3

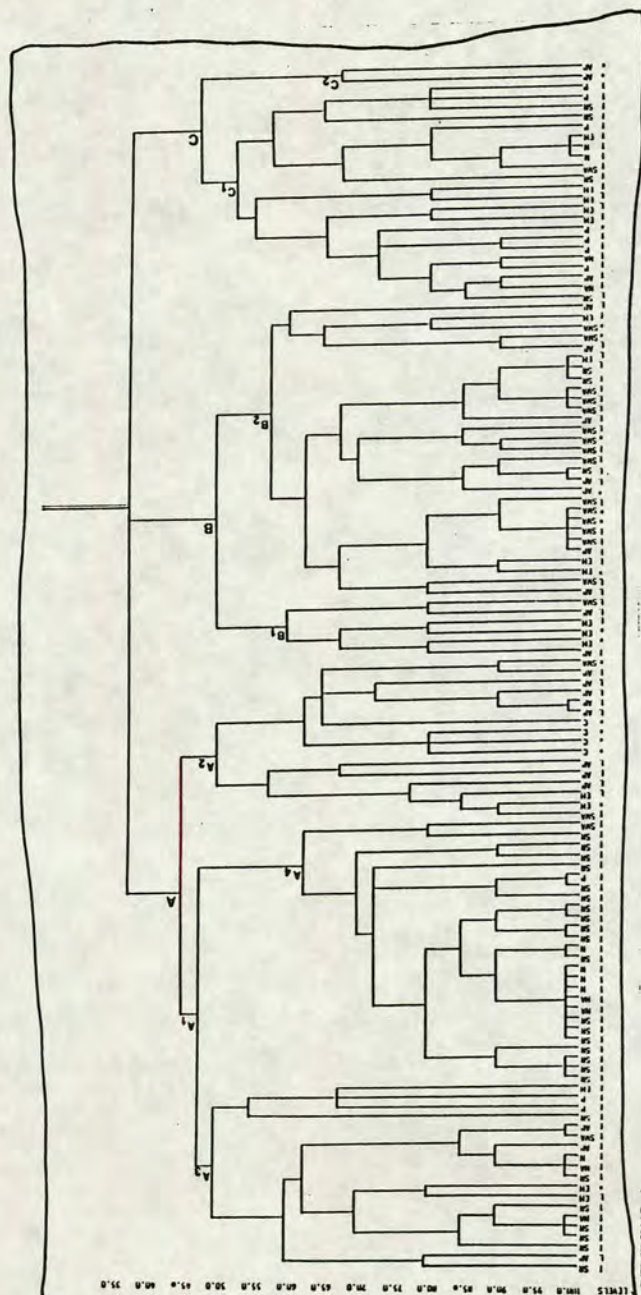


Fig. 6. Diagrammatic version of the dendrogram produced by a GENSTAT "Hierarchy" program (UPGMA method). Gower's similarity coefficient (1971) was used. The taxonomic identification of OTUs (operational taxonomic units) is given (T - *Bromus tectorum* ssp. *tectorum*; L - *Bromus tectorum* ssp. *lucidus*) as well as their geographical origin: AP - Arabian Peninsula; C - Canary Islands; EM - Mediterranean; N - Norway; NA - N Africa; P - Portugal; SR - S USSR; SWA - SW Asia.

Notes on particular features

GLUMES. The number of veins on the glumes in sect. *Genea* has traditionally been considered to be 1 for the lower and 3 for the upper with an exception for *B. sericeus* with 3 and 5(7) respectively. In plants of ssp. *tectorum* and ssp. *lucidus*, I find that this number varies not only from plant to plant, but even in the same plant. The most common combinations are 1/3, 1/4, 1/5 and 3/5, but 3/3, 3/4, 3/7 and 2/3 were also encountered.

The nervation of the lower glume seems to be a much more conservative character and therefore a more useful taxonomic tool than the nervation of the upper one. The set 1/3 veins clearly predominates in Europe and N Africa and is associated with more ssp. *tectorum*-like features. I found an increasing number of veins mainly in SW Asia as already reported, but, in addition, and for the first time, I observed the same in the Iberian Peninsula and the Canary Islands (with a higher incidence in the latter). In SW Asia, this increasing number of veins is associated most often with typical ssp. *lucidus* characters, but also with plants which, in other aspects, have an intermediate morphology, or even with typical ssp. *tectorum* characters. In the western extremity of its range this increasing number of veins is associated with ssp. *tectorum* features and in the Canary Islands with the intermediate morphologies. It seems that similar patterns of evolution may have occurred in both extremities of the overall geographic range.

Section *Bromus*, the other group of brome annuals was defined (Smith 1970) by, amongst other features, ovate glumes, the upper one 7-veined. As I see it now, these findings about *tectorum* and *lucidus* call into question the status of the existing sections in the genus. Perhaps they are less distinct than has been thought.

SYNAPTOSPERMY and CHORISPERMY. Synaptospermy, the condition where diaspores are released while physically attached to each other, was mentioned for the first time in *Bromus* by Scholz (1978), in particular for *B. sericeus*, but was never taken into account in Floras. As a contrast to synaptospermy, Scholz uses the term heterodiaspory. Heterodiaspory describes the situation where diaspores have more than one form, as is the case in *B. tectorum*. In fact, the term is not a contrast to "synaptospermy". Therefore, I use here the new term "chorispermy".

A chorispermous condition (Figs. 1, 2) exists when the florets in a single spikelet separate from each other at maturity being dispersed individually as it occurs to an extent in *B. tectorum* ssp. *tectorum*. In this taxon, all fertile florets are released separately, but the sterile ones are dispersed together with the uppermost fertile floret. Synaptospermy is the opposite condition (Figs. 3, 4): florets remain together and are dispersed as one single unit. For the florets to separate it is necessary that the rachilla axis that holds all the florets breaks

below each one. For this, a callus, as a ring around this axis, needs to develop. This is the case of ssp. *lucidus* where there is a complete callus only below the lowermost floret. In SW Asia, but sometimes in the most western area of distribution, a variably incomplete callus can be found between fertile florets, thus making it sometimes difficult to decide whether a given plant is chorispermous or synaptospermous. A false synaptospermous condition exists when there is only one fertile floret because the sterile ones disperse with the single fertile one.

In a true synaptospermous condition a question of caryopsis viability arises.

✓ Do all the grains germinate? I have observed a few herbarium specimens that grew in xeric places in which, because of the short life cycle of the plants combined with a slow rate of decomposition due to aridity, the "mother" spikelet, from which the plants germinated, has been preserved intact. The adult plant had germinated from the lowermost fertile grain and there was no sign of germination on the other ones. The synaptospermous condition is, in fact, associated with the *lucidus* kind of morphology — that means, in this particular instance, with plants more related to semi-xeric areas, being an example that can be added to the list of Saharo-Sindian synaptospermous plants cited by Murbeck (1920).

Dispersal biology seems to play a role in speciation in sct. *Genea* where different groups of taxa present clearly different strategies. In *tectorum* s.l. the whole assemblage of sterile florets and its 3-dimensional arrangement for wind-dispersal, together with synaptospermy, presents a very particular and almost unique example in this section. Therefore it has high taxonomic relevance.

Discussion

There is strong correlation between geography and the dual character states "lower glume 1-veined/chorispermy" & "lower glume 3-veined/synaptospermy". The latter is confined to SW Asia and the former distributed throughout the total range of the group — except for Saudi Arabia, S and SW Iraq and southern parts of the E Mediterranean countries.

But the existence of numerous intermediates between extremes and the fact that odd specimens in SW Asia are still not covered by these criteria supports adopting subspecific rank. As indicated in the key *B. tectorum* L. ssp. *tectorum* designates chorispermous plants with a 1-veined lower glume and *B. tectorum* L. ssp. *lucidus* synaptospermous plants with a 3-veined lower glume.

It might be argued that the great morphological variability of these plants is due to phenotypic plasticity rather than to genetic diversity, thus further weakening the case for specific rank but possibly also that for subspecific rank.

However, though it is true that these plants show strong phenotypic plasticity, this manifests itself largely in vegetative parts; the productive ones affected are only panicle size and number of spikelets. The reproductive characters here used to separate the two subspecies are thus certainly the expression of the genetic diversity of these plants. They are not phenotypic and they are not due to arrested development. Because such plants grow together there is a strong possibility of hybridisation between the 2 subspecies which, if it were proven, would further support the taxonomic treatment here proposed.

Even with this newly adopted taxonomic treatment, I found plants with combinations of character states so much in between the subspecies that it was impossible to associate them with confidence to one or the other. These intermediate taxa can be grouped in the following way:

1. Plants that in general look like typical ssp. *tectorum*, but have either 3/4 or 3/5 veins or are synaptospermous;
2. Plants that in general look like typical ssp. *lucidus*, but have 1/3 veins;
3. Plants either with glumes 1/3 or 3/5-veined and callus not completely formed;
4. Plants that in general look like ssp. *lucidus*, but have ovate-oblong glumes. (Although this is an infrequent variant this is the morphology of the lectotype of *B. sericeus*);
5. Plants that in general look like ssp. *lucidus*, but have 3-5/7 veins. (Although this is an infrequent variant it is also that of the lectotype of *B. sericeus*).

These variants grow along a strip from the western to the eastern boundary of the species range but do not expand northwards (Fig. 7). The area of greatest morphological diversity is from the E Mediterranean coast to NE Iran and this is probably the centre of origin of this group, both according to Webb's criteria (1985) and my own conclusions. Typical ssp. *tectorum* with glumes 3/5-veined is the only variant that is spread throughout this geographic range, being also the most common one.

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Fig. 7. Distribution of variants of *Bromus tectorum* which are not readily assignable to either ssp. *tectorum* or ssp. *lucidus*.

- - General ssp. *tectorum* facies but lower glume 3-veined;
- - General ssp. *tectorum* facies but synaptospermous;
- - General ssp. *lucidus* facies but lower glume 1-veined;
- ▼ - Glumes 1/3 or 3/5-veined and callus almost completely formed;
- 7 - General ssp. *lucidus* facies but ovate-oblong glumes;
- v - General ssp. *lucidus* facies but upper glume 7-veined.

All the plant material mapped/as studied.

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FINIS

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So ilka morn like a bird,
I flew doon to him and heard
O' pitcher plants and polyanths and umbels,
O' nepenthe's little trap,
O' the circulating sap,
Wi' mony a bonnie flow'r my mem'ry jumbles.
An' oft on Saturday
We turned our work to play,
An' climbed the ben or scoured the moor for species
rare and dainty;
Yet never did he tire
To name the plants we did admire,
Nor cared though there were twa or twenty.

Anonymous student of Edinburgh University, 1880 (Botanical
Society of Edinburgh News, June, 1990).